Collective decision-making in jackdaw winter roosts

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Abstract

Animals living in groups must often make decisions collectively to maintain the benefits of group cohesion. Collective movement decisions require group members to reach a consensus before departure so that individuals can coordinate and synchronise their movement timing and direction. Therefore, behavioural mechanisms must be utilised that can efficiently transfer social information and integrate a variety of individual decision preferences. Some groups use quorum mechanisms to optimise both decision-making speed and accuracy, whereby the likelihood of the group performing an action increases sharply and non-linearly after a threshold number of individuals have indicated support. Quorum decisions have been well studied in eusocial insects, but empirical evidence is lacking that they play a role in large groups of vertebrates. Acoustic cues, such as vocalisations, may provide an efficient means for individuals to indicate support and reach a consensus when many individuals are dispersed or visually obscured. In this thesis, I investigated the potential for vocally-mediated quorum decisions to coordinate collective departures in jackdaw winter roosts. Here, many hundreds of birds often perform synchronised mass take-offs around sunrise that are preceded by high levels of vocalisations. Firstly, using audio and video recordings, I found that when calling intensity increased at faster rates, departures occurred earlier and greater proportions of the roost population departed together. Similarly, greater absolute calling intensities immediately prior to departure were associated with greater proportions departing cohesively, but calling intensity was unrelated to roost group size. Secondly, I used playback experiments to test whether artificially simulating an earlier onset of consensus through greater calling intensities just before departure would cause earlier departures. Experimental calling playbacks caused departures to occur on average 5-6 minutes earlier compared to control playbacks. In contrast, departure times under natural conditions (no treatment trials) showed no clear differences with those of control trials. This indicates that jackdaws were responding specifically to conspecific calls and that calling has a causal effect on departure timing. Overall, my thesis provides the first empirical and experimental evidence for collective movements being coordinated by vocally-mediated quorum decisions in large vertebrate groups.

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Chapter 1: *General Introduction*

1.1. Collective decision-making and social information use

Collective decision-making plays a vital role in the lives of many group-living animals. Groups regularly need to make a range of important decisions, such as where to find food (Ward & Zahavi 1973; Harel *et al.* 2017) or where to nest and raise young (Seeley *et al.* 2006; Visscher 2007). By staying close to others, individuals can reduce their own risk of predation (Hass & Valenzuela 2002; Krause & Ruxton 2002) and have greater access to mates and social information (Bijleveld *et al.* 2010; Davies *et al.* 2012).

While many collective decisions can be 'self-organising', whereby group-level patterns emerge from simple, local rules and individual interactions (Couzin & Krause 2003; Sumpter 2006; Herbert-Read 2016), individuals' traits and behaviour can vary extensively and disproportionately influence decision-making (Jolles *et al.* 2017, 2020). Theoretical models of collective movement have typically treated individuals as identical and interchangeable within a group (Couzin *et al.* 2002, Couzin & Krause 2003), but individuals can vary extensively in their decision preferences (Jolles *et al.* 2020). For instance, individuals may have stronger preferences to move off due to being hungrier (Rands *et al.* 2003), bolder (Harcourt *et al.* 2009) or more informed than other group members about foraging opportunities (McComb *et al.* 2001, 2011). This can commonly lead to conflicts of interest, which need to be resolved to reach a consensus and maintain cohesion (Conradt *et al.* 2009; Conradt 2012). This may be particularly important non-kin groups where genetic interests do not align (Hamilton 1964; Lukas & Clutton-Brock 2018).

Two main ways that groups can resolve conflicts in decision preferences or information uncertainty to reach a consensus are through despotic (unshared) or democratic (shared) decision-making (Conradt & Roper 2005, 2009; King & Cowlishaw 2009). The former may emerge when individual leaders (usually informed or dominant elders) determine the activity or movement direction of all group members (Couzin *et al.* 2005; Schaerf *et al.* 2016). Notable examples include African elephant (*Loxodonta africana*) matriarchs (McComb *et al.* 2001, 2011), golden shiner fish (*Notemigonus crysoleucas*) (Reebs 2000) and ravens (*Corvus corax*) (Wright *et*

al. 2003). However, this may only optimise individual fitness in groups that are relatively small (usually <50 individuals), where information difference between individuals is large, or have closely associated networks of often related individuals (Conradt & Roper 2003). Indeed, conflicting decision preferences may be mitigated by close social affiliation with dominant individuals, such as in chacma baboons (*Papio ursinus*) (King *et al.* 2008). Here, long-term benefits of being affiliated with leaders, such as increased offspring survival (Palombit 2003) and predator protection (Cowlishaw 1994), can outweigh short-term costs, such as feeding after leaders (King *et al.* 2008). In contrast, when dominant baboons have less to gain from monopolising food sources if they are abundant and evenly distributed, shared consensus decision-making can take over (King *et al.* 2008; Strandburg-Peshkin *et al.* 2015). By pooling social information from multiple group members, democratic decision-making can average conflicting preferences and be less costly to the group overall, thus reducing the risk of group fission (Conradt & Roper 2005, 2009). While groups may split when conflict is high and social affiliation is relatively weak, baboons (Strandburg-Peshkin *et al.* 2015) and homing pigeons (*Columba livia domestica*) (Biro *et al.* 2006) often compromise and average movement direction if the difference in angle between options is small. In these cases, the benefits of group cohesion outweigh the costs of an individual not pursuing their preferred decision outcome.

1.2. Coordinating collective movements

Exchanging social information efficiently between group members through social cues is essential for coordinating cohesive collective movements, such as bird flocks (King & Sumpter 2012; Ling *et al.* 2019a), fish shoals (Ward *et al.* 2008), locust swarms (Buhl *et al.* 2006) and large migrating ungulate herds (Shellard & Mayor 2020). To maintain cohesion, collective movements such as these require both precise temporal and directional synchrony, often among many individuals (Conradt & Roper 2000; Petit & Bon 2010; Pillot *et al.* 2010; Rosenthal *et al.* 2015). Indeed, group fission can be extremely costly for individuals if a consensus cannot be reached (Krause and Ruxton 2002; Sueur *et al.* 2011; Merkle *et al.* 2015). This is particularly important for species living in unpredictable, heterogeneous environments that generally select for greater reliance on social over personal information due to increased information uncertainty (Sueur *et al.* 2011). When social cues are transmitted efficiently, new information on rich foraging locations can

propagate rapidly through a population. For instance, American bison (*Bison bison*) rapidly congregate at rich feeding sites after observing and following the movement directions of others (Merkle *et al.* 2015). Similarly, leaf-cutter ants (*Atta cephalotes*) acquire food information, follow other ants and increase foraging efficiency after head-on encounters while crowding together along foraging trails (Farji-Brener *et al.* 2010). Therefore, to maintain social cohesion over time, it is important for groups to utilise social cues that can exchange information efficiently.

The role of social cues and information transfer is particularly important in coordinating democratic decisions as groups often need to integrate conflicting individual interests to reach a consensus (Conradt & Roper 2005; Couzin *et al.* 2011). A common way individuals can communicate the extent of their motivation for a particular group decision outcome is through 'notifying' or recruitment behaviours (Petit & Bon 2010). For example, some ants leave pheromone trails that build up in concentration when visiting and returning from potential new nest sites, with higher concentration trails indicating a greater degree of support for a particular site and its relative quality (Beckers et al. 1993; Sumpter & Beekman 2003). Visual cues are another way animals can communicate preferences in consensus decisions, such as more individuals starting to move off in groups of domestic sheep (*Ovis aries*) increasing the likelihood of the whole group departing (Ramseyer *et al.* 2009a). Similarly, African buffalo (*Syncerus cafer*) (Prins 1996) and domestic cattle (*Bos taurus*) (Ramseyer *et al.* 2009b) have been observed to use body orientation and stare direction to notify others of their departure readiness and preferred direction. In cattle, more individuals became more likely to move off when there were greater numbers with their body oriented in a particular direction (Ramseyer *et al.* 2009b). Moreover, white-faced capuchin monkeys (*Cebus imitator*) are known to use backward glances to recruit others to a collective movement, which can increase the likelihood of initiating a group departure (Meunier *et al.* 2008).

Acoustic cues are also widely associated with collective movement coordination across taxa due to their efficient information transfer capabilities. In mammals, vocalisations can often be used in combination with visual cues to coordinate departures, such as white-faced capuchins producing more vocal 'trills' closer to departure (Boinski 1993; Leca *et al.* 2003). Vocalisations may be particularly useful at attracting and recruiting others when individuals are dispersed or vision is obscured, such as in group reunions of golden-brown mouse lemurs (*Microcebus*

ravelobensis) after dispersal in dense forests (Braune *et al.* 2005). Similarly, meerkats (*Suricata suricatta*) use vocal cues to coordinate group movements without needing to stop foraging and lift their head up for visual confirmation (Gall & Manser 2017). In eusocial insects, *Apis* honeybees use vibrational 'piping' signals as a necessary part of coordinating swarm departures to new nest sites (Makinson & Beekman 2014). Here, recruiting bees make 'buzz runs' through the colony and pause to emit very short sound pulses from their wings (piping) to arouse nearby bees and warm flight muscles in preparation for flight (Seeley & Tautz 2001; Visscher & Seeley 2007). In birds, some species increase their rate of vocalisations immediately prior to a collective take-off, such as in domestic geese (*Anser domesticus*) (Ramseyer *et al.* 2009c), green woodhoopoes (*Phoeniculus purpureus*) (Radford 2004) and swans (*Cygnus sp.*) (Black 1998). However, research has often struggled to distinguish between when acoustic cues are used as active signals in 'vote-casting' processes (Sueur *et al.* 2010; Sperber *et al.* 2017), and when individuals simply produce cues in correlation with increased arousal prior to moving off, such as in Verreaux's sifakas (*Propithecus verreauxi*) (Trillmich *et al.* 2004). In either case, acoustic cues likely have the inadvertent effect of raising awareness of the differing motivations of other group members' preceding and during collective movements, and thus, may play a role in facilitating cohesion.

1.3. Quorum decisions

One way animal groups make consensus decisions that efficiently optimise individual fitness and average decision preferences is through quorum mechanisms (Conradt & Roper 2005; Bose *et al.* 2017). Here, the probability of a group carrying out a particular action, such as moving off to a new foraging patch, sharply and non-linearly increases when a threshold number of individuals have indicated in favour of the action (Conradt & Roper 2005; Chittka *et al.* 2009; Conradt 2012). While some quorum decisions can require a super-majority of 'voters', such as 65% of individuals in gorillas (Stewart & Harcourt 1994) and 62% in red deer (Conradt & Roper 2003), many groups rely on sub-majority quorums (Conradt & Roper 2005). Here, groups can integrate a variety of decision preferences and social information while reducing the greater time costs associated with pooling information from many group members. Both theoretical models and empirical work indicate that this allows groups to make both fast, accurate and cohesive consensus decisions (Ward *et al.* 2008; Chittka *et al.* 2009; Sumpter & Pratt 2009), with majority decisions usually

being sub-optimal in comparison (Marshall *et al.* 2019). Through quorums, more extreme decision outcomes that only favour a very small proportion of the group can be avoided by restricting the effect on group behaviour any one individual has until a threshold of other individuals have indicated support for the same outcome (Conradt & Roper 2003). Therefore, quorums can facilitate reaching a consensus while still allowing groups to exchange a diversity of social information and make accurate decisions (Franks *et al.* 2003; Simons 2004; Sumpter & Pratt 2009). For example, *Apis* honeybee scouts perform 'waggle dances' to advertise new nest site locations, which allow information about many potential sites to be spread rapidly through the colony until a quorum number of dancers have indicated in favour of a particular site (Seeley & Visscher 2006). Moreover, in white-faced capuchins, three or more individuals initiating a movement are required for the rest of the group to follow successfully (Petit *et al.* 2009). Similarly, meerkats (*Suricata suricatta*) (Bousquet *et al.* 2011) and African wild dogs (*Lycaon pictus*) (Walker *et al.* 2017) require at least two but usually three initiators for a group movement to occur. However, in these cases, individuals use vocal cues to signal motivation, such as meerkats using specialised 'moving calls' (Bousquet *et al.* 2011) and wild dogs using sneezes (Walker *et al.* 2017).

Social context can have important implications for the variability of quorum thresholds to ensure the speed and accuracy of consensus decisions remain optimal. For example, three-spined sticklebacks (*Gasterosteus aculeatus*) exhibit varying group sizes that are associated with different threshold numbers of initiators required to trigger a collective movement away from a predator (Ward *et al.* 2008) or towards a new foraging patch (Ward *et al.* 2012). The quorum mechanism balances the risk of decision error and greater exposure to predators if individuals separate from the group prematurely, with obtaining additional information and making more accurate decisions by following others (Ward *et al.* 2012). However, smaller groups of fish have a much greater risk of error in that they are likely to be more sensitive to individual movements due to being attenuated to a greater risk of predation compared to larger groups (Ward *et al.* 2008, 2012). While larger groups make more accurate decisions, they usually require a higher threshold of initiators for the group to change direction, which reduces the likelihood of 'false alarm' errors being amplified through the whole group (Cresswell *et al.* 2000; Ward *et al.* 2008; Sempo *et al.* 2009). Therefore, the trade-offs between decision speed and accuracy have different fitness consequences for different sized groups. This could be why some

groups with highly variable group sizes adopt quorum thresholds that are proportional to the total number of individuals. For example, whirligig beetle (*Dineutes discolor*) flash expansions (Romey & Kemak 2018) and sanderling (*Calidris alba*) flock departures (Roberts 1997) require 10% of group members to indicate support, with studied group sizes ranging from 12-48 and 2-120, respectively. In contrast, quorums of absolute or fixed numbers of supporters may be more effective when group size is relatively stable, such as in meerkats (Bousquet *et al.* 2011) and wild dogs (Walker *et al.* 2017). When groups are consistently large, such as in many eusocial insects, continuous social cues that build in gradations may be more effective for assessing a consensus as here it can be difficult to assess absolute quorum numbers in favour of an action. This could be why some ants interpret pheromone trail concentrations (Cronin 2012, 2013) as proxies for when a quorum number of individuals favour a particular nest site. Similarly, honeybees seem to interpret the rate of waggle dancing as an indicator of the relative quality of each potential nest site (Seeley & Buhrman 2001; Seeley *et al.* 2006). Moreover, intra-group relatedness may influence quorum variability. Unlike eusocial insects, groups containing mostly non-kin, such as whirligig beetles, may also have higher quorum thresholds as individual preferences likely differ to greater extents. Individuals may be less sensitive to the actions of unrelated conspecifics as kin selection benefits would not present (Hamilton 1964; Romey & Kemak 2018). This may also be the case when personal association strength determines the efficiency of social information transfer (Ling *et al.* 2019b).

Ecological context can also influence the variability of quorum thresholds. For instance, experimental studies have shown that ant colonies regularly tune the quorum threshold required to initiate a collective move to a new nest site depending on the urgency. Quorums tended to be lower when nest sites had been destroyed and the colony were left exposed, requiring fewer scouts to accumulate at a particular nest site (Franks *et al.* 2013). Similarly, quorums were lower where the presence of predators or harsh winds were simulated using olfactory cues (Franks *et al.* 2003) as the colony was vulnerable, prioritising decision speed over accuracy. Variable predation risk also effects decision-making in guppies (*Poecilia reticulata*), where laboratory experiments have shown that males coming from high predation environments that attempted to access females made slower, more cautious decisions (Burns & Rodd 2008; Chittka *et al.* 2009). This may have important implications for quorum decisions in cases when animal groups must make

movement decisions that may involve exposing themselves to predators. In typically high predation risk environments, quorum thresholds may become higher to increase decision time and accuracy when pooling information about the presence of a predator before deciding to move off.

1.4. Avian communal roosts and collective departures

Many bird species gather in large numbers to rest together (often overnight) in communally established sites called roosts, which are one of the most well studied examples of collective behaviour in nature (Ward & Zahavi 1973; Eiserer 1984; Beauchamp 1999; Bijleveld *et al.* 2010). While some species only roost in relatively small numbers (<50 birds), such as house finches (*Carpodacus mexicanus*) (Dhondt et al. 2007) and green woodhoopoes (*Phoeniculus purpureus*) (du Plessis & Williams 1994), others can form roosts of many tens of thousands, such as barn swallows (*Hirundo rustica*) (Verma 2010), European starlings (*Sturnus vulgaris*) (Ward & Zahavi 1973; Clergeau & Fourcy 2005) and some corvids (Coombs 1961a, 1961b; Clayton & Emery 2007). Communal roosting may provide numerous fitness benefits for individuals, such as decreased predation risk per capita and increased predator detection (Krause & Ruxton 2002), reduced thermoregulation costs (Hatchwell *et al.* 2009; Shipley *et al.* 2019), and greater access to social information and greater foraging success (Ward & Zahavi 1993; Bijleveld *et al.* 2010). Indeed, the 'information centre hypothesis' was proposed as a primary driver for the evolution of roosting behaviour, whereby social information about foraging opportunities could be actively advertised and spread between many individuals (Ward & Zahavi 1973). Roosting may have evolved because advertising the roost to newcomers and actively sharing information to uninformed individuals via recruitment calls and aerial displays (Marzluff et al. 1996; Wright *et al.* 2003) can improve foraging success by maximising the number of birds searching for food in the area (Ward & Zahavi 1973). This may be particularly beneficial when resources are scarce or patchy (Templeton & Giraldeau 1996) and may be why many birds form roosts in the harsher wintertime (Coombs 1961a; Meanley 1965; Shipley *et al.* 2019). However, it is more likely that information is shared through inadvertent cues (Bijleveld *et al.* 2010). For instance, individuals may be more inclined to follow seemingly successful foragers that may be carrying food remains in their beak or claws, in good body condition or making energetic flight behaviour (Mock et al. 1988). Arriving earlier at the roost may also indicate that an individual's daily food energy intake had been met after foraging

successfully (Bijleveld *et al.* 2010). Empirical evidence in ravens (*Corvus corax*) (Wright *et al.* 2003) and hooded crows (*Corvus corvix*) (Sonerud *et al.* 2001) showed that information on new foraging opportunities could be spread rapidly to uninformed individuals when they roosted close to and followed informed conspecifics. Moreover, information on predator proximity may be spread rapidly through the roost by fright behaviour or vocalisations (Griffin 2004; Bijleveld *et al.* 2010).

Communal roosts often perform mass departures from the roost that require precise coordination and synchronisation to avoid group fission. Examples of birds that perform collective roost departures include red-billed quelea (*Quelea quelea*) (Ward 1965; Ward & Zahavi 1973), black vultures (*Coragyps atratus*) (Rabenold 1987) and many corvids, including ravens (*Corvus corvix*) (Marzluff et al. 1996), rooks (*Corvus frugilegus*) and jackdaws (*Corvus monedula*) (Coombs 1961a; Hubálek 2017). Observations in queleas, grackles (*Quiscalus sp.*), starlings and ravens have noted that birds often vocalise loudly and continuously while assembling at the roost at dusk until after dark and then begin vocalising again before departure around sunrise (Ward & Zahavi 1973; Wright *et al.* 2003). It is possible that vocalisations may provide an efficient means of exchanging social information between many dispersed, visually obscured individuals and assessing the 'collective mood' (see for definition: Ward & Zahavi 1973) in the context of roost departure decisions. Indeed, vocalisations are commonly associated with avian collective departures from resting spots, such as in Canada geese (*Branta canadensis*) winter roosts (Raveling 1969), and groups of domestic geese (*Anser domesticus*) (Ramseyer *et al.* 2009c) and swans (*Cygnus sp.*) (Black 1988). However, whether birds use vocally-mediated quorum decisions to coordinate mass departures from communal roosts is not yet fully understood. So far, *Apis* honeybee waggle-dances, and subsequent piping behaviour, provide the only evidence of acoustically-mediated coordination of large group departures that are comparable to avian roost departures in scale (Visscher & Seeley 2007).

1.5. Study system

Jackdaws (*Corvus monedula*) are highly sociable corvids that present an ideal study system for investigating collective decision-making in large vertebrate groups. In the winter, they form large winter roosts with rooks (*Corvus frugilegus*) and often carry out mass roost departures around sunrise (Coombs 1961a). Jackdaws are also highly vocal and rely heavily on flexible communication and social information

exchange between individuals in a variety of social and decision-making contexts. For instance, ‘contact calls’ are used to identify conspecifics (Stowell *et al.* 2018), allowing individuals to respond accordingly with their relative position in the colony’s linear dominance hierarchy (Röell 1978; Lee *et al.* 2019). Vocal cues are also important for monogamous jackdaw pairs when coordinating nest-building and tracking the location of their partners (Hahn *et al.* 2020).

In the context of collective behaviour, jackdaws rely heavily on vocalisations to recruit others when initiating anti-predator mobbing. Here, both caller numbers and identity play important roles in the collective decision-making process. Indeed, greater numbers of individuals performing ‘scolding calls’ are more likely to attract more recruits to mobbing events (Coomes *et al.* 2019). Similarly, resident nestbox jackdaws and members of the studied colony are more likely to attract more recruits in their residential area than non-colony members and rooks, with females attracting even fewer due to generally having lower social ranks (Woods *et al.* 2018). These examples highlight that jackdaws possess the ability to discriminate a range of conspecific characteristics from vocal cues alone, which can lead to different collective behavioural responses. However, in collective departures from roosts containing many hundreds of birds calling simultaneously, there are likely cognitive limitations that heavily constrain vocal discrimination of individual callers (Ditz & Neider 2016; Coomes *et al.* 2019).

So far, research on jackdaw roosts has suggested that vocalisations may play a significant coordinating role in collective roost departures due to the increase in the rate of calling or ‘chatter’ that occurs leading up to morning departures (Pearce 2012; Bridger 2016). However, no studies have yet to find evidence for vocalisations causally influencing collective departure decisions, even after the effect of different call types (frequency, Hz) was tested experimentally (Bridger 2016). Moreover, jackdaws have a history of prominent roosting behaviour in Cornwall (Coombs 1961a, 1961b), making the area surrounding the University of Exeter’s Penryn Campus especially suitable for locating and studying active roost sites. Therefore, in combination with the unique social organisation of jackdaw roosts, this makes them an ideal species for investigating questions on collective decision-making at avian roosts, and in large vertebrate groups more generally.

1.6. Research aims

This thesis contains two chapters that investigate whether jackdaws use vocalisation-based quorum decision-making to coordinate collective departures from their winter roosts. In Chapter 1, I used video footage and audio recordings of vocalisations to test the predictions that increasing calling intensity leading up to departure produces (i) earlier departures and (ii) greater proportions of all roosting birds departing together. I also investigated whether greater absolute calling intensity in the final minute before departure is associated with greater proportions departing together, and whether it is influenced by group size. In Chapter 2, I used playback experiments with multiple loudspeakers to test the prediction that greater intensities of calling introduced just before departure cause earlier departures.

1.7. Relevance of my research

Collective decision-making forms a fundamental part of understanding why many animals can live together in stable groups. It is an evolutionary adaptation for promoting sustainable group cohesion that allows individuals to reap benefits from group living while also resolving inevitable conflicts of interest that arise (Conradt 2012; Bose *et al.* 2017). Studying the mechanistic explanations underlying collective decisions is crucial to understanding how behaviour is translated from individuals to group or 'superorganism' characteristics (Seeley 1989; Petit & Bon 2010; Sasaki & Pratt 2018; Ling *et al.* 2019c). Revealing how these mechanisms operate in nature may also provide important insights into collective behaviour dynamics in humans. For instance, modelling the movement decisions of individual birds within a flock shows significant parallels with and implications for human crowd control (Helbing *et al.* 2000; Dyer *et al.* 2008), including the effects of individuals' social affiliation or information (Drury 2020). Similarly, human architecture has often taken inspiration from the collective nest-building efforts of social insects, such as termites, bees and ants, through the study of biomimetic architecture (Penn & Turner 2018).

Collective behaviour is often very difficult to study in the wild. This is especially the case when tracking the movements of many individual decision-makers, or when studying groups that travel great distances very quickly, such as bird flocks. However, theoretical models and laboratory studies can only simulate the complexities of wild systems to a certain extent; therefore, there has been a recent push for more field studies and experimental work (King *et al.* 2018). There is also a

substantial gap in research concerning the collective decision-making of large vertebrate groups, particularly the role of acoustic cues in quorum decisions and coordinating group movements. I hope this thesis will help broaden our understanding of collective decision-making across more taxa and different group sizes, as well as bridging the gap between theoretical and empirical research in collective behaviour as a whole (Giardina 2008; King *et al.* 2018).

Chapter 2: *Vocalisations appear to mediate quorum decisions in collective roost departures*

Abstract

To remain cohesive, animal groups must collectively decide on the timing and direction of their movements. Many species use quorums to coordinate collective decisions, whereby decisions are made when a threshold number of supporting individuals have favoured a particular action. While empirical work on quorum decisions is well supported in eusocial insects, there is less support for quorums decision-making mechanisms in large vertebrate groups. Vocalisations may be an efficient way for large groups to transfer social information between many dispersed individuals, thereby promoting group cohesion during collective movements. Jackdaw winter roosts offer an ideal study system for investigating vocally-mediated quorum mechanisms as they perform mass roost departures around sunrise that are often preceded by a growing chorus of calls from hundreds to thousands of individuals. To test whether vocalisations play a role in coordinating collective roost departures, I made audio and video recordings of morning departure events. While accounting for meteorological effects, I tested whether the rate of increase in calling intensity was associated with the timing and cohesiveness of group departures. When the rate of increase in calling intensity was greater, departures occurred earlier and were more cohesive, with larger proportions of the roost departing together. The latter relationship was non-linear, consistent with a quorum decision-making mechanism. The calling intensity in the final minute before departure was predictive of the cohesiveness of departures, but unrelated to the total group size, suggesting that a quorum threshold might be based on a fixed intensity of calling. These results indicate that jackdaws rely on vocal cues to coordinate mass roost departures and highlight the potential role of vocally-mediated quorums in the decision-making of large vertebrate groups.

2.1. Introduction

Collective decisions must be coordinated effectively if animal groups are to balance and integrate an array of individual preferences to maintain cohesion (Conradt 2012; Miller *et al.* 2013). By reaching a consensus and staying in a cohesive group, individuals can reap substantial fitness benefits, such as reduced predation risk, access to mating opportunities and social information about foraging opportunities (Ward & Zahavi 1973; McComb *et al.* 2001; Krause & Ruxton 2002; Wright *et al.* 2003; Davies *et al.* 2012). Reaching a consensus is particularly important for group movement decisions, which require participating individuals to agree on the timing and direction of the collective action (Conradt & Roper 2010). If a group fails to reach a consensus, group fission could occur, resulting in individuals losing the benefits of group living (Krause & Ruxton 2002; Davies *et al.* 2012). Therefore, efficient communication and social information transfer that promote group synchrony and cohesion may reduce the likelihood of individuals incurring these costs when on the move (Kerth 2010; Sueur *et al.* 2011).

One way some animal groups achieve consensus and synchronous action is through the use of quorums. Quorum decision-making involves animals deciding on an option only after a threshold number of individuals have indicated in favour (Conradt & Roper 2005; Bose *et al.* 2017). The quorum could represent the majority of the group (majority decision), or a sub or super-majority of individuals within the group (Conradt & Roper 2003, 2005). Once reached, quorum thresholds are typically indicated by a sharp, non-linear increase in the probability of a certain action being adopted by the whole group (Conradt 2012). Many theoretical models and empirical studies indicate that quorum responses optimise both decision speed and accuracy (Ward *et al.* 2008; Chittka *et al.* 2009; Sumpter & Pratt 2009). Experimental evidence in social insects supports this: for instance, *Apis* honeybees can assess many potential nest sites simultaneously and rapidly coordinate swarm departures through a quorum mechanism. Indeed, bee scouts advertise nest locations through ‘waggle dances’, which trigger rapid colony-wide movement to a new site when a quorum number of scouts advertise the same nest (von Frisch 1967; Seeley & Visscher 2004; Riley *et al.* 2005). Similarly, *Temnothorax* ant scouts recruit others to new nest sites through tandem runs and after a quorum number of ants have accumulated at a nest, switch to rapid transport runs where the passive majority of ants are physically carried to the new nest (Pratt *et al.* 2002; Pratt 2005; Franks *et al.* 2015). Other ants

combine quorum numbers of ants accumulating at a given nest with pheromone trails that allow nestmates to navigate independently between different potential sites, following pheromone concentration as an indicator of site popularity (Cronin 2012). There have also been some studies in vertebrate groups showing that coordination of collective movement decisions can be achieved through quorums. For example, there is strong experimental evidence in three-spined stickleback shoals (*Gasterosteus aculeatus*) (Ward *et al.* 2012), and suggestive evidence in sanderling flocks (Roberts 1997) and white-faced capuchin monkeys (*Cebus imitator*) (Petit *et al.* 2009), that groups synchronise movement to new foraging patches after a threshold number of initiator individuals have moved off. Moreover, there is anecdotal evidence from observational work in Hamadryas baboons (*Papio hamadryas*) (Kummer 1968) and African buffalo (*Syncerus cafer*) (Prins 1996) that body posture and gaze direction may be important in some quorum-based 'vote-casting' decisions to signal movement direction preference. Most studies investigating quorum decision-making have been in relatively small groups. However, when groups are large and dispersed, it may become more difficult to visually track and integrate the movement of a relatively small number of initiators. Therefore, what communication mechanisms could large groups use to assess the preferred actions of other group members?

Vocalisations, which can propagate over long distances, may provide an efficient means of promoting quorum-based decisions, especially in visually obscuring environments, such as woodlands (Radford 2004; Braune *et al.* 2005). To date, research investigating the role of vocalisations in coordinating collective decisions has been mostly in relatively small mammal groups (<50 individuals). For instance, many studies of primate group decisions have shown that group members signal their motivation to move off through grunts or trills (Stewart & Harcourt 1994; Leca *et al.* 2003; Sperber *et al.* 2017), but here, quorum decision-making was not tested explicitly. Studies providing evidence for acoustically-mediated quorum decisions have been limited. For example, strong experimental evidence in meerkats (*Suricata suricatta*) (Bousquet *et al.* 2011) and correlative observational evidence in African wild dogs (*Lycaon pictus*) (Walker *et al.* 2017) show adherence to a vocally-mediated quorum through specialised 'moving calls' and 'sneezes', respectively. Here, a threshold number of callers is required to initiate group departures: at least two but usually three individuals in both wild dogs (Walker *et al.* 2017) and meerkats (Bousquet *et al.* 2011). To my knowledge, the only large animal group (>50

individuals) known to use acoustic cues in association with quorum decisions is the honeybee (mean colony size of 11800, ranging from 2400 to 41000 individuals: Fell *et al.* 1977). Here, bees likely encode information on new nest or food locations and their quality through vibrational wingbeats and sound pulses incorporated in waggle dances (Towne 1985; Nieh & Tautz 2000; Łopuch & Tofilski 2020). Moreover, once a quorum of waggle dancers advertising the same nest site has been reached, scouts use vibrational 'piping' signals that spread through the colony and build in a crescendo, priming the swarm for take-off by warming flight muscles (Seeley & Tautz 2001; Visscher & Seeley 2007). However, the potential for acoustic signals to actively facilitate quorum-based decisions has yet to be investigated in large vertebrate groups. While flocks of starlings (*Sturnus vulgaris*), grackles (*Quiscalus quiscula*) and red-billed queleas (*Quelea quelea*) have been observed to display loud vocalisation choruses prior to departures from their roosting site (Ward & Zahavi 1973), it is not known whether the intensity or rate of vocalisations predicts departure timing and cohesiveness. Indeed, research has shown that bird groups display more intense calling closer to departure, such as in green woodhoopoes (*Phoeniculus purpureus*) (Radford 2004), geese (Raveling 1969; Rameseyer *et al.* 2009b) and swans (Black 1988). This suggests that calling intensity might reflect the group's proximity to reaching a consensus. However, despite vocalisations being fundamental in the social lives of birds, most studies have been based on relatively small groups that have yet to determine through audio recordings how the acoustic properties of vocalisations may play a role in the preparation and initiation of collective departures.

One of the most spectacular examples of collective movement in large bird groups occurs in jackdaws (*Corvus monedula*), highly sociable members of the corvid family. During the winter, they form large woodland roosts containing up to thousands of individuals (Coombs 1961). Around sunrise, they produce intensive bouts of calling that appear to grow in intensity preceding a mass departure from the roost (Pearce 2012; Bridger 2016). As roosting individuals will exhibit substantial variation in energetic and informational states, as determined by previous success in locating profitable foraging patches (Bijleveld *et al.* 2010), this is likely to generate pronounced differences in preferences regarding the timing and direction of departure. For instance, individuals may be more motivated to leave the roost earlier if they fed less successfully the previous day, increasing search time and ensuring their ideal food intake is met. Moreover, birds who fed more successfully the day

before may be the first to leave the roost if they already possess first-hand information on rich feeding sites. Uninformed individuals may instead prefer to wait to follow in synchrony with informed conspecifics to benefit from the social information inadvertently transmitted by their departure direction (Bijleveld *et al.* 2010). Departing together may also provide important benefits in terms of reduced per capita predation risk from group dilution and detection effects (Dehn 1990; Davies *et al.* 2012). Given that the presence of large groups of vocalising birds in predictable locations may attract predators, synchronous departures may be an adaptation for individuals to offset the risk of predation. Having left the vicinity of the roost, where one may expect predation risk is highest, these large departure flocks then break up into smaller feeding flocks (Tast & Rassi 1973; Röell 1978). To achieve synchronous departures and maximise the benefits of grouping, decision-making mechanisms are therefore required that can integrate a range of preferences from many individuals spread across a large area. Previous observations suggest that the intensity of calling in jackdaw roosts increases in a crescendo preceding departure (Pearce 2012; Bridger 2016), raising the possibility that departure timing is coordinated by a vocalisation-based quorum mechanism. However, this trend has yet to be confirmed across a greater variety of roost sites with varying population sizes. Despite vocalisations being vital in coordinating collective anti-predator responses in jackdaws (in the form of mobbing calls: Woods *et al.* 2018; Coomes *et al.* 2019), their role in coordinating group departures remains unclear.

In jackdaw roosts, collective departure decisions could be mediated through both the absolute calling intensity immediately prior to departure and how quickly calling intensity builds over time. Support for a departure could build to a quorum based on absolute calling intensity acting as a proxy for a quorum number of supporters, eliminating the need to identify and track individual caller numbers while in very large groups. However, the rate of increase in calling intensity may also play a salient role in the decision-making process. For instance, individuals on the peripheries may not experience the same acoustic stimulus as those in the centre due to sound attenuation, which could make it more difficult to identify an absolute threshold. Indeed, research has shown that greater rates of calling are associated with reaching consensus and maintaining social cohesion, with individuals being more likely to stay together during a collective departure. For example, pairs of pale-winged starling (*Onychognathus nabouroup*) are more likely to both fly away, instead of none or only one, when the calling rhythms they exchange increase at faster rates

(Hausberger *et al.* 2020). Whether reaching a quorum of absolute or rate of calling intensity is the final trigger for a departure, I expect positive non-linear relationships with the extent that group members stay together upon departure, as found in other species, such as meerkats (Bousquet *et al.* 2011) and wild dogs (Walker *et al.* 2017). Moreover, in the case of a quorum of absolute calling intensity, it is also unclear whether this would be fixed relative to group size, such as meerkats requiring at least two to three vocalising individuals (Bousquet *et al.* 2011), or proportional, such as whirligig beetles requiring 10% of individuals displaying startle responses before the group rapidly disperses (Romey & Kemak 2018). In species that form large groups but also have considerable variation in group size, such as jackdaws, a small, fixed threshold might result in more false positive responses (Cresswell *et al.* 2000). Decision error may then increase further as group size increases, leading to greater chances of costly group fission. In addition, as jackdaw roosts are mostly made up of non-kin, it is likely that a relatively high threshold must be maintained compared to kin groups, such as cooperative breeders like meerkats. If individuals are surrounded by large numbers of unrelated individuals, there may be greater genetic conflicts of interest (Hamilton 1964; Romey & Kemak 2018). Therefore, a proportional quorum in jackdaw roosts may be more appropriate for maintaining optimal decision speed and accuracy across a wide range of group sizes.

Here, using a combination of audio and video recordings at multiple roost sites of different sizes, I investigated whether jackdaws' collective roost departures at sunrise are coordinated by vocal cues and asked whether there was evidence for a quorum decision-making mechanism. Specifically, I tested the following predictions:

(1) If vocalisations are important in a decision to leave, greater rates of increase in calling intensity will be associated with earlier departures. Since jackdaws vocalise almost continuously for many hours leading up to departure, the speed at which vocalisations build up over time could reflect if, or how quickly, consensus is reached among group members. This may then impact decisions of departure timing.

(2) Both the rate of increase in calling intensity and the absolute calling intensity in the final minute before departure will have a positive non-linear relationship with the cohesiveness of departures (i.e. the proportion of the total roost population departing together).

(3) The calling intensity in the final minute before departure will be higher in roosts with larger populations, indicative of a proportional quorum in relation to group size.

As previous studies indicate meteorological variables, such as rainfall, cloud coverage, wind speed, barometric air pressure, air humidity and temperature are important in influencing avian roost departures, I accounted for them in my analyses (Reebs 1986; Doucette & Reebs 1994; Khadraoui & Toews 2015; Bridger 2016; Hubálek 2017).

2.2. Methods

2.2.1. Roost Sites

Observations of jackdaw collective departures were carried out across nine roost sites in Cornwall, UK during the winter periods: Nov 2018 - Mar 2019 and Nov 2019 - Feb 2020. Roosts were located at a minimum of 2.78 km from each other, except for two roosts located within the same woodland but 300 m apart. Pilot observations were carried out prior to any data collection to confirm whether roost sites were active and what times departures occurred to inform subsequent visits. Active roosts were recognised and selected by the following criteria: (1) consisted of at least 50 birds and (2) jackdaws settled at and departed from roughly the same position each day. These observations confirmed that the two roosts within the same woodland could be treated as independent, as both the timings of departures and the jackdaws' direction of travel differed consistently between them.

2.2.2. Data Collection

Departure time

Starting an hour before sunrise, collective departures were observed with binoculars, filmed using a Canon EOS 550D camera with a 70-300 mm lens and departure times were recorded (N = 55). To avoid disturbance, observations were made at least 50 m away from standardised positions with a clear view of departures. Collective departures were defined as more than ten jackdaws flying away from the roost at the same time in the same direction. Video footage was used to count the number of birds in each departure and to identify the time of the largest departing group of birds. As roost departure times in corvids correlate strongly with sunrise time (Khadraoui & Toews 2015; Hubálek 2017), I calculated departure time relative to

sunrise, with negative values indicating minutes before sunrise. Sunrise times at the nearest village/town to the roost (max. distance: 4.20 km) were recorded each day from the UK Met Office's online forecasts (www.metoffice.gov.uk).

I defined and quantified departure cohesiveness as the proportion of the total roost population that the largest departing group made up. To enable analyses of the cohesiveness of group departures, I used video footage to count the number of birds in every collective departure and the total number occupying the roost. To ensure accurate counts, videos were reviewed frame-by-frame in Adobe Photoshop. Counts were then verified by someone not informed about the hypotheses of this study by recounting 16% of videoed departures, covering five roosts of varying population sizes. A high degree of inter-rater reliability was found, with an intra-correlation coefficient (ICC) of 0.999 ($p < 0.001$) and a 95% confidence interval of 0.995 and 1.

Audio recordings

Recorders were programmed to record for four hours, starting three hours before sunrise. In the winter of 2018/2019, I used six SM3 Wildlife Acoustics recorders, but equipment failures meant only four were available in 2019/2020. Recorders were strapped to trees within the roost at a height of 2.5 m and positioned in a grid 40 m apart. Before attaching them to trees, I placed the recorders together, activated them and used loud hand claps to produce clear acoustic signals that could later be used to synchronise the audio files (.wav) from all the recorders in Audacity (www.audacityteam.org). I also applied 6 dB noise reduction to all recordings in Audacity to reduce the amplitude of continuous background sounds that were independent from jackdaw calls but existed in the same frequency range. This reduced the amplitude of continuous hums or buzzes picked up on the recorder microphones while leaving jackdaw calls unaffected.

Meteorological variables

For each observation day, I noted whether there was any rainfall. Data for barometric air pressure (mPa), cloud coverage (%), wind speed (mph), air temperature (°C), and air humidity (%) were obtained for each roost's GPS location to the nearest hour to departure time through an application programming interface (API) from 'World Weather Online' (www.worldweatheronline.com).

2.2.3. Data and Statistical Analysis

All statistical analyses were carried out in R version 1.1.456 (R Core Team 2018).

Model construction

Mixed effects models were built using *lme4* (Bates *et al.* 2015) and *lmerTest* (Kuznetsova *et al.* 2017). Residual plots were assessed for violations of model assumptions. I tested for multicollinearity between predictors by assessing the variance inflation factor (VIF). To construct models containing all combinations of potentially important explanatory variables and generate objective measures of which variable combinations best predicted the response term, I used the *dredge* function from the *MuMin* package (Barton 2009). 'Dredging' was only performed because all variables in the analyses have clear biological rationales and any combination of variables is, in principle, biologically plausible. To avoid fixed effect bias when estimating variance components, all linear mixed effects models (LMMs) were fitted by maximum likelihood (ML) before model selection. However, I refitted the final, best-fitting model by restricted maximum likelihood (REML) to minimize small sample size bias and prevent inflation of type-I errors (McNeish 2017). I then generated regression coefficients of the best-fitting model using the *ggeffects* package (Lüdecke 2018), which I plotted, along with the raw data, using the *ggplot2* package (Wickham 2016). Roost site was fitted as a random effect in all mixed model analyses.

Model selection

Model selection was carried out using an information theoretic (IT) approach and models were ranked by Akaike's information criterion corrected for small sample sizes (lowest to highest AICc), using the methods put forward by Richards *et al.* (2011). Models that had a Δ AICc ≤ 6 made up the 'top set' and were included in model selection tables. I then implemented the 'nesting rule', described by Richards (2008), whereby models in the top set that were more complex versions of nested, better performing models with lower AICc were disregarded. More complex models were only retained when their AICc was at least 2 less than a simpler, nested model.

Acoustic spectrum analysis of jackdaw calls

To determine the rate of change in calling intensity leading up to departure, I performed spectrum analyses in MATLAB (MathWorks, version 2019b) on acoustic data from mornings where both audio recordings and departure times were successfully obtained. This used a restricted data set (N = 30 mornings, across six roosts) as some audio recordings could not be used due to equipment failures or heavy rain and wind masking jackdaw calls. To calculate calling intensity, I first calculated estimates of the power spectral density (PSD) of the recordings within one-second time windows. PSD captures the power (here, in dB) of each frequency component (Hz) of the signal. Here, I restricted PSD calculations to the frequency range of jackdaw calls (480-4000 Hz), which I defined as the calling intensity. This allowed me to investigate changes in the calling intensity in the hour leading up to the largest collective departure. For each recorder, I also calculated normalised PSD estimates, so that each one-second PSD value in the hour period was converted into values between zero and one, relative to the lowest and highest PSD values. This was done to account for differences in the sensitivities of recorders or differences in the distance they were placed from the roost.

To calculate the rate of increase in calling intensity, I calculated linear regression slope estimates for each hour recording, where normalised PSDs were modelled as a function of time (hrs). To measure the mean calling intensity in the final minute before departure, I also calculated single absolute PSD estimates for the final minute of each hour recording. To test whether pre-departure changes in the intensity of sounds that were not jackdaw calls, such as from strong winds or road traffic, predicted departure time or cohesiveness, I quantified levels of background noise by calculating PSD estimates for low frequency noise outside the range of jackdaw vocalisations (0-400 Hz). Estimates were calculated both for each second of the hour period and as a single estimate over the last minute prior to departure. Per-second PSDs for low frequency noise were then normalised as before and used to calculate regression slope estimates for each hour recording. These slope estimates were included as covariates in analyses where relevant, as background noise, such as road traffic, could potentially influence patterns of calling and departure, as well as the reliability of absolute values of calling intensity.

Influences on departure time

I used linear mixed effects models (LMMs) to test the influence of seven meteorological variables on the time of the largest departure relative to sunrise (N = 55). Mornings with rain or heavy cloud cover would have lower light levels, which could cause birds to wait longer than normal before departure until light conditions are more favourable for flight and navigation. Rain and strong winds could also inhibit the propagation of acoustic cues and the delay the decision of when to depart. Rain and wind could also impact flight performance and increase the energetic costs, potentially causing birds remain at the roost longer and conserve energy. Similarly, low barometric air pressure, high humidity and low temperature can all reduce the amount of lift generated by a bird's wings, therefore making flight under these conditions more energetically costly. Indeed, birds are known to be sensitive to subtle changes here (Metcalfe *et al.* 2013).

Analyses also included measures of the total number of birds in the roost and the size and shape of the roosting area as covariates, as these may influence information transfer across the roost. I used satellite images from Google Maps to estimate the roosting area (m^2) and the irregularity/complexity of the shape of the roost (estimated using the fractal dimension index: Mandelbrot 1967). Uncertainty in counts of bird numbers or estimates of the boundary of some roosting areas meant that LMMs incorporating these covariates had to use a subset of the data (N = 45).

To test whether departures occurred earlier if calling intensity increased at faster rates, I ran a separate model on the subset of data (N = 30) for which acoustic data were available. Departure time relative to sunrise was fitted as the response variable, with rate of increase in calling intensity as the key explanatory variable. The important predictors identified in the best-fitting model in the initial analysis above were included as covariates along with the rate of increase in low frequency background noise.

Influences on departure cohesiveness

Using the full dataset (N = 44), wind speed, rainfall, air temperature and total roost population were included as predictors to determine their potential influence on departure cohesiveness and social information transfer. For instance, rain and wind could affect the propagation of acoustic cues, potentially constraining the group's

ability to reach a consensus and maintain cohesion. Greater wind speeds could also influence flight conditions whereby birds may be more inclined to stay together when departing to reduce the risk of becoming separated from the group and vulnerable to predators. Moreover, colder temperatures could cause birds to roost closer together for thermoregulatory benefits, potentially increasing the speed and fidelity that social information could be exchanged. Conversely, a greater total roost population could mean birds distribute themselves over a larger area, potentially hindering the propagation of vocalisations and ability to perceive a consensus. Indeed, in domestic geese (Ramseyer *et al.* 2009c) and black-headed gulls (*Larus ridibundus*) (de Schutter 1997), when roosting individuals were spread out over a larger area the number of birds in a collective take-off was lower. Roost area size and shape irregularity may also have similar effects. Therefore, I examined these variables as additional covariates in separate models using a subset of the data due to values not being available (N = 27).

To test whether birds departed more cohesively when the rate of increase in calling intensity was greater, I ran a series of generalised linear mixed models (GLMMs) with a binomial error structure (N = 30). The response variable was the proportion of birds that left together, with the number of birds in the largest departure as the numerator and the total number of roosting birds as the denominator. The rate of increase in calling intensity across the hour period before departure was included as the key predictor. If any predictors were significant from the initial analysis with the full dataset, they were included as covariates along with the rate of increase in low frequency background noise.

To test whether departure cohesiveness is determined by calling having reached a threshold intensity just before departure, I ran a binomial GLMM with the proportion of all birds in the largest departure as the response variable (as above) and the absolute calling intensity in the final minute as the key explanatory variable (N = 35). To establish whether reaching a consensus through an acoustic threshold of calling may be dependent on group size, additional LMMs tested whether the calling intensity in the final minute was predicted by the total number of roosting birds. These analyses considered only data from mornings where roost departures contained >50% of the roost population departing together as these are likely indicative of mornings where a consensus decision was reached (N = 21). Variables that could introduce errors in measures of calling intensity (background noise levels,

wind speed and whether there was rain) were investigated as additional covariates. To avoid any measurement errors caused by differences in the sensitivity of recorders within roosts, these analyses used absolute intensity values from the same centrally-placed recorder for each morning. Additional analyses examining the influence of calling intensity over the last 30s or five minutes prior to departure produced qualitatively the same results as those using the final minute prior to departure, so only the final minute is reported here.

2.3. Results

2.3.1. Influences on collective departure time

Across 55 mornings and 9 roost sites, the departure time of the largest group ranged from 45 minutes before sunrise to 15 minutes after (mean (± s.e.) = 20.4 (1.4) mins before sunrise), demonstrating large variation in the time birds decided to leave the roost.

Meteorological influences on departure time

The largest departure from the roost occurred earlier relative to sunrise when barometric air pressure was higher, but departures occurred later when there was greater cloud coverage and when there was rain (Figure 2.1). Barometric air pressure, cloud coverage and rainfall were all included in the retained, best-fitting model out of the 15 models making up the 'top set' (Table 2.1, 2.2). Air temperature, wind speed and air humidity also featured in the top set, but these effects were not robust (temperature: estimate (± s.e.) = -0.552 (0.459), lower/upper conf. interval = -1.428/0.323, p = 0.234; wind: estimate (± s.e.) = 0.116 (0.112), lower/upper conf. interval = -0.099/0.328, p = 0.307; humidity: estimate (± s.e.) = 0.188 (0.126), lower/upper conf. interval = -0.048/0.434, p = 0.142).

Table 2.1. LMMs that make up the 'top set' (Δ AICc ≤ 6) of models predicting roost departure time relative to sunrise from meteorological variables. Fixed effect headings refer to the variables barometric air pressure (mPa) as 'baro'; cloud coverage as 'cloud'; air humidity (%) as 'humid'; whether it rained before departure as 'rain'; average air temperature (°C) as 'temp'; and average wind speed (mph) as 'wind'. The presence of numeric variables in the model are represented by their model estimate coefficients and the categorical variable by the '+' symbol. The retained, best-fitting model is highlighted in bold.

model	intercept	baro	cloud	humid	rain	temp	wind	df	logLik	AICc	Δ AICc	retained	weight
12	**149.744**	**-0.176**	**0.107**	NA	**+**	NA	NA	**6**	**-177.72**	**369.20**	**0.00**	**yes**	**0.19**
28	162.573	-0.184	0.117	NA	+	-0.552	NA	7	-176.94	370.27	1.07	no	0.11
44	116.347	-0.145	0.103	NA	+	NA	0.115	7	-177.15	370.69	1.49	no	0.09
60	119.385	-0.143	0.115	NA	+	-0.738	0.165	8	-175.81	370.76	1.56	no	0.09
43	-32.367	NA	0.118	NA	+	NA	0.183	6	-178.70	371.15	1.96	no	0.07
64	111.953	-0.149	0.111	0.189	+	-1.036	0.252	9	-174.58	371.16	1.96	no	0.07
59	-27.212	NA	0.130	NA	+	-0.748	0.232	7	-177.40	371.19	1.99	no	0.07
11	-30.313	NA	0.130	NA	+	NA	NA	5	-180.24	371.69	2.50	no	0.05
16	151.935	-0.181	0.105	0.037	+	NA	NA	7	-177.67	371.71	2.52	no	0.05
63	-40.359	NA	0.127	0.179	+	-1.033	0.318	8	-176.35	371.84	2.64	no	0.05
32	168.807	-0.196	0.115	0.075	+	-0.631	NA	8	-176.71	372.55	3.35	no	0.04
48	112.406	-0.148	0.099	0.088	+	NA	0.146	8	-176.85	372.84	3.64	no	0.03
27	-26.830	NA	0.139	NA	+	-0.457	NA	6	-179.75	373.24	4.04	no	0.03
47	-38.979	NA	0.115	0.078	+	NA	0.212	7	-178.48	373.34	4.14	no	0.02
15	-29.757	NA	0.130	-0.007	+	NA	NA	6	-180.23	374.22	5.02	no	0.02

Table 2.2. Summary statistics of the best-fitting model predicting relative departure time from meteorological variables. The conditional R^2 estimate is provided in the first row and estimates the proportion of variance explained by both fixed and random effects (Nakagawa & Schielzeth 2013). The marginal R^2 estimate is provided in the second row and estimates the variance explained by only the fixed effects. Thereafter, semi-partial R^2 estimates are provided for individual fixed effects and the random effect. Statistically significant variables ($p < 0.05$) are denoted by the * symbol.

variable	estimate	95% CI (lower)	95% CI (upper)	s.e.	*t*-value	*p*-value	R^2 estimate	variance	s.d.
model 12 summary								0.791	
fixed effects								0.382	
intercept	149.093	-6.997	308.106	81.273	1.83	0.073			
baro	-0.175	-0.330	-0.023	0.079	-2.21	0.032*	0.038		
cloud	0.107	0.050	0.162	0.029	3.71	<0.001*	0.088		
rain	9.112	4.980	13.170	2.112	4.32	<0.001*	0.120		
random effects							0.409		
roost							0.409	53.55	7.32

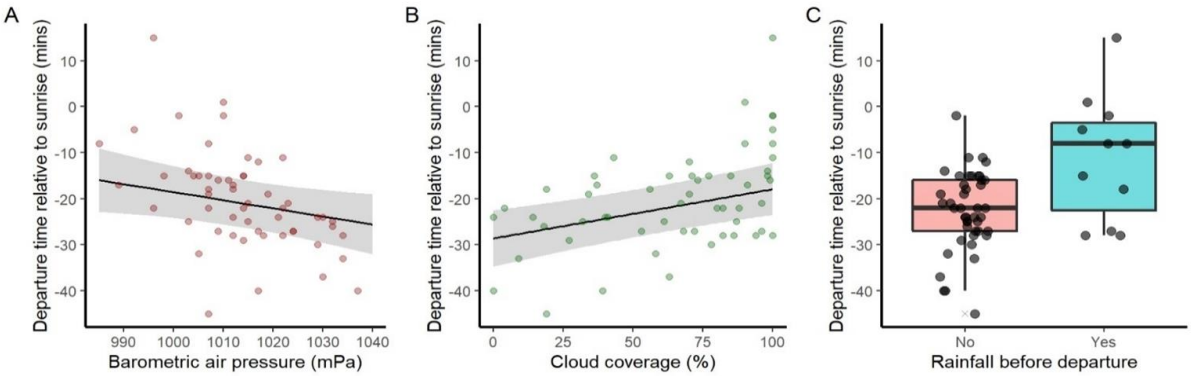


Figure 2.1. Effects of the three meteorological variables in the best-fitting model on departure time relative to sunrise (mins): (A) barometric air pressure (mPa), (B) cloud coverage (%) and (C) whether it rained before departure. For (A) and (B), solid black regression lines and shaded 95% confidence interval bands are displayed along with the raw data points and were generated using model estimates from the best-fitting model. For (C), boxplots represent the median, quartiles and range of the raw data (overlayed as black points) for each category.

Roost size, area and shape influences on departure time

Accounting for the influences of the meteorological variables in Table 2.2, departure times were not associated with the total number of roosting birds (estimate (± s.e.) = -0.002 (0.008), p = 0.763), roosting area size (estimate (± s.e.) = 0.007 (0.006), p = 0.282) nor roost shape irregularity (estimate (± s.e.) = 257.1 (208.2), p = 0.269).

Influence of calling intensity on departure time

Calling intensity often increased throughout the hour prior to departure (Figure 2.2.A), but there was substantial variability in calling patterns across roosts (Figure 2.2.B). LMM analyses showed that roost departures occurred earlier when the rate of increase in calling intensity was greater (Figure 2.3). Seven models were present in the 'top set' (Table 2.3). The retained, best-fitting model contained the rate of increase in calling intensity, as well as cloud coverage and whether there was rain before departure (Table 2.4). There was no evidence that changes in low frequency background noise influenced departure time when this variable was added to those from the best-fitting model (estimate (± s.e.) = -5.533 (8.967), p = 0.543).

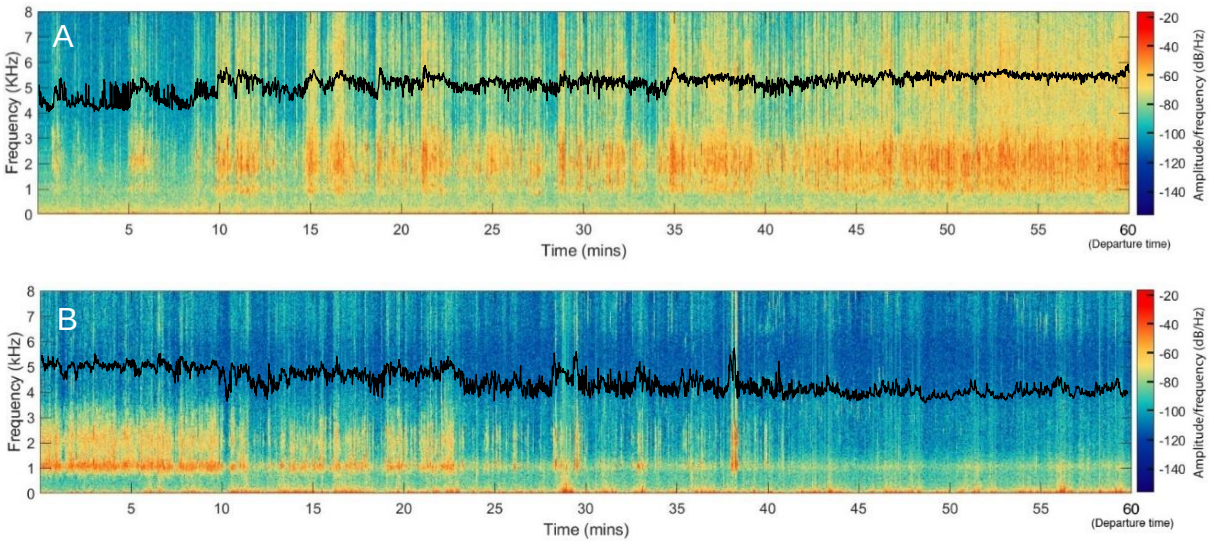


Figure 2.2. Spectrograms of jackdaw calling during the one-hour period leading up to departure. These exemplify the variation in calling patterns between two different mornings and roosts, showing that calling can (A) increase (per second: estimate (± s.e.) = 0.004 (0.000), lower/upper conf. interval = 0.004/0.004, t = 53.589, p < 0.001, R^2 = 0.444) (N = 22), and (B) decrease (per second: estimate (± s.e.) = -0.006 (0.000), lower/upper conf. interval = -0.006/-0.006, t = -69.609, p < 0.001, R^2 = 0.574) (N = 8) linearly leading up to departure. Amplitude/frequency (dB/Hz) represents the intensity of sound at each frequency level and is displayed as a colour heat map, with red colours indicating the loudest signals. The black lines represent the relationship between the change in calling intensity over time for the jackdaw frequency range (480-4000 Hz) and correspond exclusively with the amplitude/frequency (dB/Hz) y-axis, showing an increase in calling intensity in (A) and a decrease in (B). Plots were produced in MATLAB (MathWorks, version 2019b).

Table 2.3. LMMs that make up the 'top set' (Δ AICc ≤ 6) of models predicting roost departure time relative to sunrise from the rate of increase in calling intensity ('slope call'), rate of increase in low frequency background noise ('slope noise') and the meteorological variables present in the best-fitting model from Table 2.1. The retained, best-fitting model is highlighted in bold.

model	intercept	baro	cloud	rain	slope call	slope noise	df	logLik	AICc	Δ AICc	retained	weight
15	**-31.188**	**NA**	**0.127**	**+**	**-18.325**	**NA**	**6**	**-89.18**	**194.02**	**0.00**	**yes**	**0.68**
31	-30.839	NA	0.129	+	-18.665	-5.847	7	-88.94	196.98	2.96	no	0.15
16	-0.630	-0.030	0.123	+	-17.938	NA	7	-89.10	197.29	3.27	no	0.13

Table 2.4. Summary statistics for the best-fitting model from Table 2.3.

variable	estimate	95% CI (lower)	95% CI (upper)	s.e.	*t*-value	*p*-value	R^2 estimate	variance	s.d.
model 15 summary							0.885		
fixed effects							0.613		
intercept	-31.165	-37.275	-24.959	3.189	-9.77	<0.001*			
cloud	0.167	0.069	0.186	0.030	4.18	<0.001*	0.167		
rain									
no									
yes	11.066	6.690	15.292	2.245	4.93	<0.001*	0.259		
slope	-18.213	-26.294	-9.617	4.573	-3.98	<0.001*	0.393		
random effects							0.272		
roost							0.272	37.14	6.10

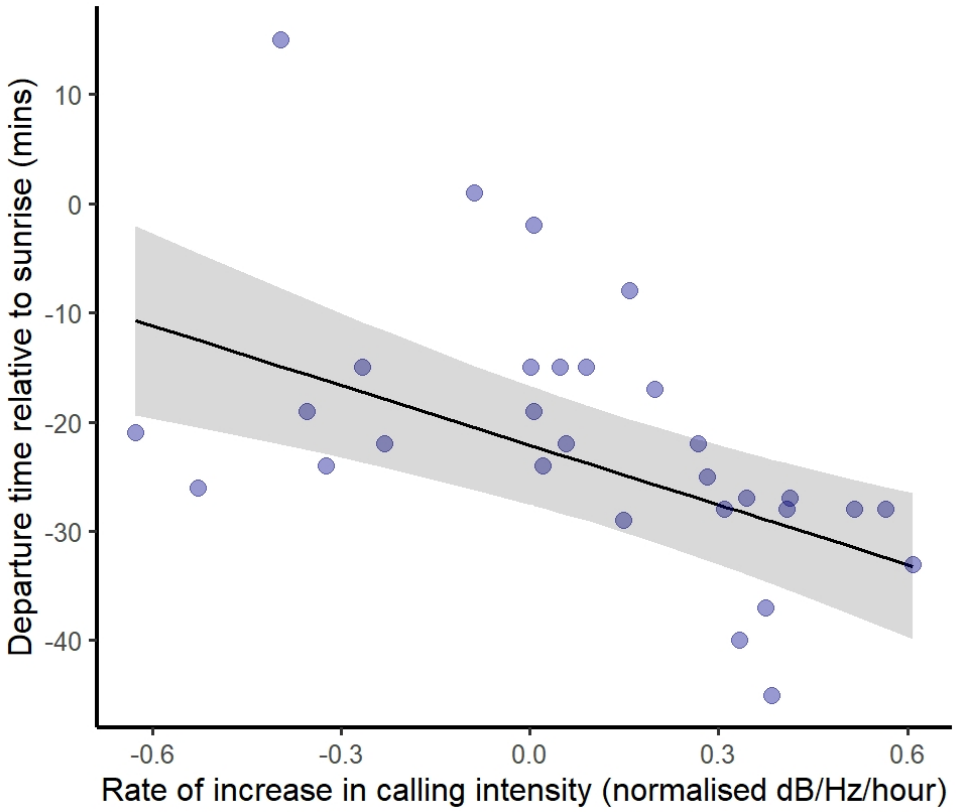


Figure 2.3. Relationship between the rate of change in calling power spectral density (PSD) leading up to departure and departure time relative to sunrise (mins). Regression line and shaded 95% confidence intervals are displayed along with the raw data points and were generated using coefficient estimates from the best-fitting LMM. Positive departure times indicate departures after sunrise, and negative departure times indicate departures before sunrise. Increased calling rates are correlated with earlier departure times.

2.3.2. Influences on collective departure cohesiveness

Across 43 mornings and eight roost sites, the proportion of the roost that left simultaneously in the largest departure ranged from 7.68% to 100% (mean (± s.e.) = 65.8 (5.2)). The estimated total number of roosting birds ranged from 159 to 1470 (mean (± s.e.) = 621 (47)), and the number of birds in the largest departure ranged from 15 to 1409 (mean (± s.e.) = 426 (50)). In an analysis with the full dataset (N=44), no meteorological variables nor the total roost population size influenced departure cohesiveness. After applying the nesting rule, the best-fitting model here contained no predictor variables (intercept: estimate (± s.e.) = 1.077 (0.819), p = 0.188). Therefore, these variables were not included in any further analyses that modelled departure cohesiveness as the response variable.

How do changes in calling intensity influence the proportion of the roost population departing together?

The rate of increase in calling intensity was a strong predictor of departure cohesiveness, with a greater proportion of the roost departing in the largest departure when calling intensity increased at faster rates (Table 2.5; Figure 2.4). This relationship was non-linear, with a sharp increase in cohesiveness when the rate of increase in calling intensity was positive, rather than flat or negative. Only 30 mornings across six roost sites generated suitably high-quality audio data and were used for this analysis.

When analysing the rate of increase in low frequency background noises (>400 Hz) as a covariate, it had no significant relationship with departure cohesiveness (estimate (± s.e.) = -0.765, z = -0.146, p = 0.884), whereas the rate of increase in calling intensity remained a strong predictor (estimate (± s.e.) = -7.836, z = -2.67, p =

Table 2.5. Summary statistics for the best-fitting model predicting departure cohesiveness from the rate of increase in calling intensity. This analysis did not detect variation at the level of the roost. This may be linked to the relatively small sample size of roosts (N = 30 datapoints across six roosts) and that the effects of variation in calling intensity as an explanatory factor in the analysis may mask variation linked to roosts.

variable	estimate	95% CI (lower)	95% CI (upper)	s.e.	*z*-value	*p*-value	R^2 estimate	variance	s.d.
model 3 summary							0.660		
fixed effects							0.660		
intercept	-0.123	-1.367	0.960	0.567	-0.217	0.828			
slope	7.734	3.383	15.116	2.826	2.737	0.006*			
random effects							<0.001		
roost							<0.001	0.00	0.00

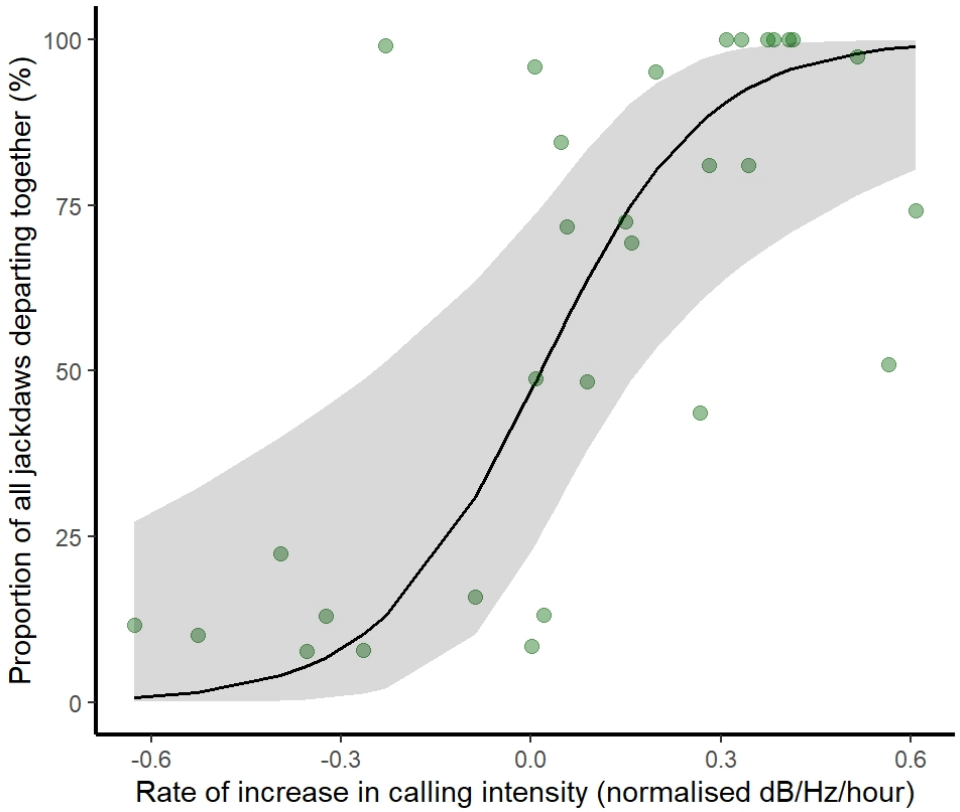


Figure 2.4. Non-linear relationship between the rate of increase in calling intensity leading up to departure and the proportion of the total jackdaw roost population in the largest departure. Rate of increase in calling intensity increases sharply when it is >0 dB/Hz/hour. Non-linear regression line and shaded 95% confidence intervals are displayed along with the raw data points and were generated using coefficient estimates from the best-fitting binomial GLMM.

0.008). Using a subset of the data for which accurate measures were available (N = 27), I found no relationships between departure cohesiveness and roost area size (estimate (± s.e.) = 1.906e-04 (0.001), p = 0.887) or shape irregularity (estimate (± s.e.) = -28.370 (70.650), p = 0.688) when modelled as covariates with the rate of increase in calling intensity (estimate (± s.e.) = 8.232 (3.193), p = 0.010).

Departure cohesiveness increased when the absolute calling intensity in the last minute before departure was higher (estimate (± s.e.) = 4.975 (1.843), z = 2.70, p = 0.007), with departures being substantially more cohesive at greater calling intensities (Figure 2.5). Cohesiveness increased more rapidly when calling intensity was >-74 dB/Hz, with the overall trend following a non-linear relationship. However, contrary to my predictions, on mornings when mass departures occurred (when >50% of the birds left together), the calling intensity in the last minute before departure did not correlate with a greater total number of roosting birds (estimate (± s.e.) = -0.002 (0.003), p = 0.726; Figure 2.6). However, calling intensity did increase with greater background noise levels in the last minute (estimate (± s.e.) = 0.361

(0.107), t = 3.37, p = 0.004) and when there was rain (estimate (± s.e.) = 7.358 (2.565), t = 2.87, p = 0.011), but decreased with greater wind speeds (estimate (± s.e.) = -0.281 (0.130), t = -2.17, p = 0.045).

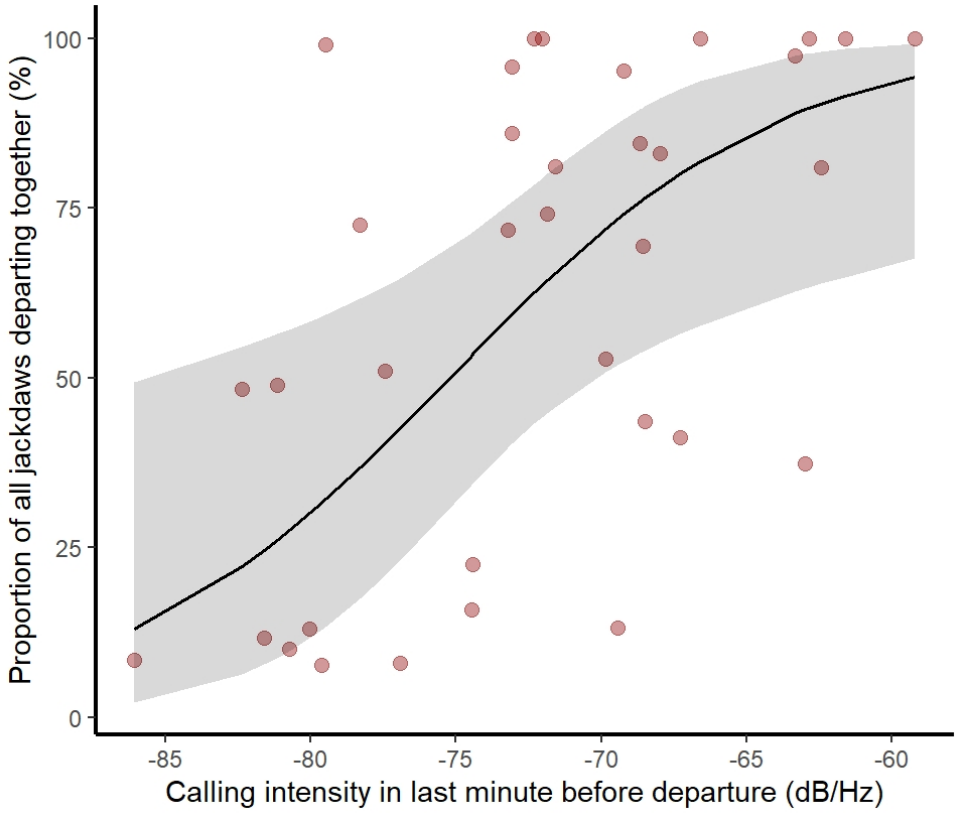


Figure 2.5. Non-linear relationship between calling intensity in the final minute before departure and the proportion of the jackdaw roost population in the largest departure. Calling intensity increases sharply when it is >-74 dB/Hz. Non-linear regression line and shaded 95% confidence interval bands are based on binomial GLMM coefficient estimates.

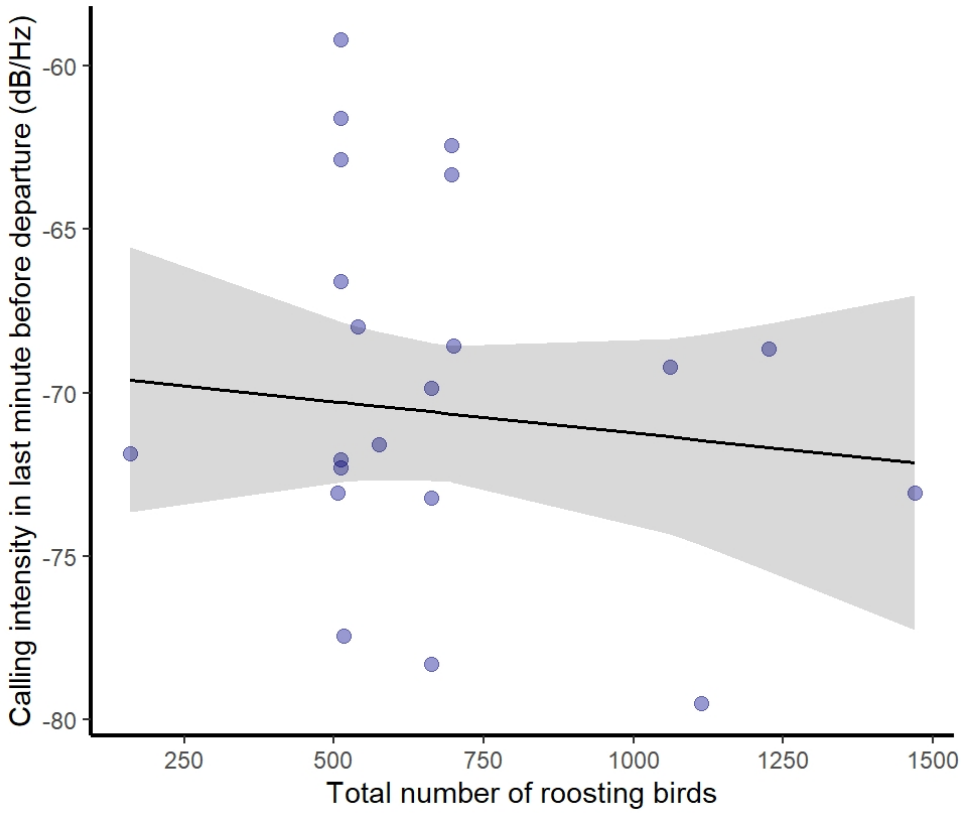


Figure 2.6. Absence of a relationship between the total number of birds and the calling intensity in the final minute before departure. Regression line and shaded 95% confidence interval bands are based on the coefficient estimates of the best-fitting LMM containing the total number of birds variable.

2.4. Discussion

This study is the first to investigate and provide observational evidence for the role of vocally-mediated mechanisms in the collective decision-making of large groups of wild vertebrates. My results suggest the use of vocalisation-based quorum decision-making in the collective departures at jackdaw roosts. As has been noted by other observers (Pearce 2012; Bridger 2016), jackdaws often exhibited a growing crescendo of vocalisations prior to collective departures from the roost. As predicted, when calling intensity increased at faster rates, the largest departure occurred earlier and was more cohesive, with a greater proportion of the roost population leaving simultaneously. More cohesive departures were also associated with greater absolute calling intensity in the final minute prior to departure. However, contrary to my predictions, when high-cohesion departures occurred (>50% of the roost population departing together), calling intensity in the final minute was not associated with roost population size. This is suggestive of adherence to a fixed quorum threshold of calling intensity in relation to group size. Overall, these results

demonstrate that jackdaws make collective decisions that are highly responsive to changes in social cues.

My results provide evidence that both meteorological variables and social interactions modulated through vocalisations influence the timing of collective departures. I found that departures occurred later on cloudier days and when it rained. As suggested by previous studies, lower light levels on cloudier and rainy days may cause birds to wait for more favourable light conditions before take-off, potentially to aid flight navigation (Reebs 1986; Doucette & Reebs 1994; Bridger 2016; Hubálek 2017). It is also possible that rain could impact flight performance on take-off, as well as inhibit the propagation of acoustic signals (Lengagne & Slater 2002). The latter could reduce the reliability of acoustic communication and introduce greater uncertainty and inefficiency in vocally-mediated consensus decision-making, leading to later departures. There was also some indication that departures occurred earlier when barometric air pressures were higher, which contrasts with previous work on jackdaw roosts where limited support for this effect was found (Hubálek 2017). This also contrasts with the implications of studies showing that low barometric air pressure causes greater feeding activity as it is associated with the onset of bad or stormy weather (Breuner *et al.* 2013; Metcalfe *et al.* 2013). Indeed, under low air pressure conditions, I would have expected birds to be more inclined to depart the roost earlier to increase feeding time and intake as finding food is more difficult during bad weather. Therefore, direct measurements of barometric air pressure at precise roost locations are needed to confirm that the direction and strength of its effect on departure time is consistent. Accounting for these meteorological variables, vocalisation patterns were strongly associated with departure time, as mass departures occurred earlier when the intensity of vocalisations increased at faster rates. It is possible that rapid build-ups of calling in a crescendo pattern serve to heighten and synchronise individuals' arousal levels (Stewart & Harcourt 1994; Ramseyer *et al.* 2009c; Hausberger *et al.* 2020), leading to consensus decisions being made sooner when vocal cues build-up faster. Indeed, similar increases in activity before the collective movements of fishes have also been observed as a means of coordinating departure timing and maintaining group cohesion, where more active groups made earlier departures (Ward *et al.* 2013).

The degree of group cohesion upon departure seemed primarily driven by the exchange of social cues. Indeed, the rate of increase in calling intensity leading up to

departure was the strongest correlate of departure cohesiveness, with meteorological variables, roost population size and roosting area size or shape having no clear influence. The relationship between vocalisation patterns and departure cohesiveness appeared to follow a non-linear relationship, suggesting a quorum threshold at the point where rates of increase in calling intensity shift from negative to positive. At this point, there was a sharp increase in departure cohesiveness, with small increases in the rate of increase in calling intensity being associated with large increases in the proportion of the roost population departing together. This pattern is predicted by theoretical models of quorum-based group decisions (Conradt 2012), and similar to other empirical findings: for example, ants switch to rapidly carrying nestmates to a new nest site after a quorum number of recruits have accumulated there following individually-led tandem runs (Pratt 2005; Davies *et al.* 2012). It is also worth noting that Hausberger *et al.* (2020) found in pairs of pale-winged starlings that neither individuals departed when there was no increase in the rate of calling rhythms exchanged, whereas greater rates of increase were more likely to lead to both individuals departing together. This greatly resembles the sharp increase in departure cohesiveness I found in jackdaws when rates of increase in calling intensity became positive. It is possible that in the absence of reliable visual confirmation of supporting numbers, jackdaws assess if the strength of these auditory signals is increasing, thereby informing their decision to leave. The strong relationship with departure cohesiveness here is also suggestive of changes in vocalisations being a more reliable means for birds to perceive a consensus than an absolute calling intensity threshold, particularly considering the differences in acoustic stimulus experienced by many dispersed individuals. Indeed, individuals would only need to assess the relative change in call production rates, without assessing the total number of birds that were calling.

Despite the potential sensory limitations of an absolute acoustic threshold, my analysis of the impact of vocalisations immediately prior to departure raises the possibility that departure decisions are linked to a fixed quorum of calling intensity relative to roost population size. Indeed, greater calling intensity in the final minute before departure was associated with greater departure cohesiveness but did not correlate with total group size. Calling intensity and cohesiveness followed a non-linear relationship and indicated a potential quorum when calling intensity was >-74 dB/Hz, with a sharp increase in cohesiveness here. As calling intensity did not vary with roost population size, this suggests that the quorum may be fixed relative to

group size. This contrasts with my predictions and previous findings of proportional quorums in relatively large groups (Roberts 1997; Romey & Kemak 2018). However, my findings do correspond with those in honeybee swarms, which require a fixed number of 10-20 scouts waggle dancing for the same potential nest site to initiate piping signalling and a colony relocation (Seeley & Visscher 2003; 2004). When group sizes vary extensively, it might be easier for individuals to detect and respond to an absolute threshold of calling intensity rather than determining intensity as a proportional value. Indeed, jackdaws may not be able to estimate the group size they are in, especially in very large groups with thousands of individuals situated in woodland roosts. However, given the relatively small sample sizes and the measurement error associated with using a single centrally-placed recorder to capture the amplitude of vocalisations, conclusions regarding absolute, fixed quorums must be interpreted with caution. For instance, calling intensity in the final minute before departure was greater when background noise was higher. So, it is possible that recordings were sensitive to varying degrees of measurement error on different days depending on how much background interference was being picked up. Arguably, this could also be attributed to jackdaws calling more loudly to compensate for more noise in their surrounding environment. Nevertheless, taken together, my results for the influences on departure cohesiveness provide compelling evidence that both the rate of increase in calling intensity and the final, absolute calling intensity reached are associated with movement decisions during roost departures. This indicates that the potential for greater rates of calling to facilitate consensus decision-making by allowing the group to reach an absolute quorum faster is still an important possibility to consider.

Although my results highlight clear patterns consistent with vocally-mediated consensus decision-making, there was also considerable variation in calling patterns, departure timing and departure cohesiveness both between roosts and across mornings at the same roost. This is likely to be linked to unmeasured variables. For instance, although I found no effect of total roost population size, and overall roost area size and shape, it is possible that the spatial distribution of birds within the roost could influence the extent to which individuals are exposed to and can respond to acoustic signals (Fernández-Juricic & Kacelnik 2004). Similarly, patterns of social association strength within the group could also influence how efficiently decisions are made (Voelkl & Noe 2008; Sueur *et al.* 2013). For example, greater numbers of jackdaw pairs in transit flocks reduce the efficiency of social

information transfer as birds pay more attention to their partner than others (Ling *et al.* 2019b). This attention-bias suggests that jackdaw may also be unlikely to be responsive to cues from other bird species' calls. Indeed, from personal observations and audio recordings, rooks often vocalised loudly but rarely were calls as prominent or continuous as jackdaw calls, and generally rooks departed earlier and separately. In contrast, small passerine birds sometimes began their dawn choruses just before jackdaws departed, suggesting that these choruses have the potential to be used as a cue for when to depart, even if on many mornings they began after departure. Furthermore, roosting jackdaws may vary in their day-to-day informational state (Couzin *et al.* 2011; Conradt 2012). Indeed, research in hooded crows (*Corvus cornix*) has shown that greater proportions of informed individuals at the roost are more likely to attract greater numbers of uninformed individuals to follow them to previously successful foraging patches (Sonerud *et al.* 2001). If there is a greater following of informed individuals, identified inadvertently by honest signals of successful feeding (Bijleveld *et al.* 2010), such as body fatness, vocalisation intensity or energetic flight displays, roost departures may become more cohesive. Conversely, in cases where individuals have differing but equally reliable information, they may be more likely to discount social information and group fissioning could occur (Couzin et al. 2005, 2011; Biro *et al.* 2006; Merkle *et al.* 2015). This might begin to explain why on some mornings jackdaws departed in separate sub-groups rather than all together, even at the same roost. As a result of differing informational states, individuals will inevitably also vary in their daily food intake. This could influence individuals' motivation for the timing of departure to ensure their energy requirements are met, which could then be conveyed through their vocalisations. Since greater intake rates are thought to be linked to earlier roost arrivals at dusk (Bijleveld *et al.* 2010), future work could account for the potential effect of energy intake variation on calling patterns by analysing arrival time in the evening as a predictor of departure time the following morning. Despite the considerable variation in calling patterns and roosting behaviour, my results still show clear correlational patterns between vocalisations and collective decision-making; however, experiments are still needed to confirm whether vocalisations play a causal role here (Holland 1986).

One possibility that deserves further investigation is that distinct aspects of social information may govern pre-departure behaviour and the departure itself, as has been suggested in other species. For instance, honeybees use acoustic piping

signals to prime swarms for departure to a new nest, but enough bees taking off pre-emptively on the periphery could be the final trigger for swarm departures (Visscher & Seeley 2007). In jackdaw roosts, I observed that birds seemed to display increased flight activity over the roosting area closer to departure time, lifting off briefly from the roost before landing again. This could reflect an increase in the occurrence of failed departures, where birds take-off but are not followed by enough conspecifics to trigger a mass departure, and therefore they return to the roost. A consequence of increasing frequency of failed departures over time may be that birds gain increasing access to movement cues as light levels increase closer to sunrise. This may provide an alternative aspect of social information that jackdaws use to assess the 'collective mood' (Ward & Zahavi 1973) and perceive a consensus. I also suggest that the build-up of calls may stimulate greater movement among roosting jackdaws. As light levels increase closer to sunrise, these movements may become more salient and thus the final decision to leave could be triggered by a combination effect of movement cues and an acoustic threshold. Future work could analyse recordings of calling immediately prior to departure to reveal whether calling intensity is lower when the light level at departure time is higher, using a low light lux meter for measurements. If so, this could suggest that when birds are departing in lighter conditions, they may rely more on visual cues, and so vocal cue production may drop as it is energetically costly.

This chapter presents empirical support for a vocalisation-based quorum mechanism playing a significant role in coordinating collective departures from jackdaw roosts. Jackdaws made earlier and more cohesive departures when calling intensity increased at faster rates, highlighting the responsiveness of their collective behaviour to changes in social cues. Indeed, greater departure cohesiveness became increasingly more likely after rates of increase in calling intensity became positive, consistent with a quorum response. Similarly, departure cohesiveness increased with greater absolute calling intensity in the final minute irrespective of roost population size, suggesting that the decision to leave may be associated with reaching a fixed quorum of calling intensity. However, it is also possible that additional visual information from individual movements is important in the final departure decision. Nevertheless, these results provide the first suggestion that vocally-mediated quorums play a significant role in the collective decision-making of large vertebrate groups, but experiments are needed to confirm if vocalisations are causally linked with the decision-making process. Understanding how information

from different sensory domains can be integrated to facilitate consensus decision-making is a clear priority for future research.

Chapter 3: *Mass roost departures are triggered earlier by playbacks of jackdaw calls*

Abstract

Staying as a cohesive group during collective movements requires behavioural mechanisms that facilitate the transfer of social information, allowing individuals to identify when a consensus has been reached. To coordinate collective decisions, many species rely on quorums, whereby a decision is made once a threshold number of individuals have favoured a particular action. Quorum decisions based on an acoustic threshold may be a particularly efficient method for maintaining group cohesion in large, dispersed groups where access to visual cues is reduced. While experimental evidence for acoustically-mediated quorum decisions is limited to relatively small groups of cooperative breeders, observational studies suggest their importance in coordinating mass departures from jackdaw winter roosts. These roosts can consist of hundreds to thousands of individuals, spread across thousands of square meters of woodland, vocalising for many hours before departure. Experimental evidence that vocalisations have a causal influence on departures, however, is lacking. Here, I used playback experiments to test whether vocal cues can trigger earlier collective departures in jackdaw roosts. As predicted, I found that experimental playbacks of jackdaw calling caused departures to occur earlier compared to control playbacks. Moreover, control playbacks caused no significant change in departure timing compared to natural departures where no playbacks were used, indicating that jackdaws were specifically responding to conspecific calls. My results provide the first experimental evidence of a vocalisation-based quorum mechanism playing a causal role in the coordination of collective movements in large vertebrate groups. This could have important implications for how flexible the decision-making process is under varying social, ecological or anthropogenic pressures.

3.1. Introduction

Animal groups that make decisions collectively must use mechanisms that facilitate the synchronisation of individuals' behaviour if they are to preserve the benefits of grouping, such as reduced risk in predation and greater access to mates and social information (Ward & Zahavi 1973; McComb *et al.* 2001; Bijleveld *et al.* 2010; Davies *et al.* 2012; Miller *et al.* 2013). Some groups use quorums to identify when consensuses have been reached, whereby a minimum number of individuals favouring an action is required for the entire group to adopt this action (Conradt & Roper 2005; Bose *et al.* 2017). Once a threshold number of individuals have indicated support, the likelihood of individuals participating in a group action becomes increasingly greater (Conradt & Roper 2005; Sumpter & Pratt 2009; Conradt 2012; Bose *et al.* 2017). Through quorums, groups can quickly and accurately integrate and average differences in decision preferences arising from individual variation in energetic or informational state (Davies *et al.* 2012; Miller *et al.* 2013), thereby promoting a consensus.

To track the decision preferences of others and coordinate collective movements, group members can use both visual and acoustic cues (Sperber *et al.* 2017). For example, suggestive evidence indicates that golden snub-nosed monkeys (*Rhinopithecus roxellana*) signal movement direction preference through body orientation (Wang *et al.* 2020). Alternatively, in some species, sharp increases in vocalisation rates can occur immediately prior to a collective departure, potentially to attract the attention of others and prepare the group to move off, such as in domestic geese (*Anser domesticus*) (Ramseyer *et al.* 2009c), green woodhoopoes (*Phoeniculus purpureus*) (Radford 2004) and swans (*Cygnus sp.*) (Black 1998). Other observational studies have revealed correlational relationships between greater rates of vocalisations and the probability of a collective movement being imminent, such as in red-fronted lemurs (*Eulemur rufifrons*) (Sperber *et al.* 2017), African wild dogs (*Lycaon pictus*) (Walker *et al.* 2017) and mountain gorillas (*Gorilla beringei beringei*) (Stewart & Harcourt 1994). This indicates that vocalisation rates may signal how many individuals are in favour of moving off, with Walker *et al.* (2017) finding evidence that a quorum number of usually three callers is required to initiate group movement. Some species appear to utilise a combination of visual and acoustic signals to convey decision preferences. White-faced capuchin monkeys (*Cebus imitator*), for example, perform a combination of backward glances and

vocalised ‘trills’ that increase the likelihood of a collective movement being initiated (Leca *et al.* 2003; Meunier *et al.* 2008). However, it is often not clear to what relative extents distinct aspects of social information govern collective decisions. Indeed, very few studies have been able to distinguish whether, instead of directly mediating consensus decisions, vocalisation rates simply increase in correlation with an impending departure to ensure group members maintain synchrony and cohesion as they move off (Trillmich *et al.* 2004). Thus, causal evidence through experimental studies is required to determine whether changes in vocalisation rates pre-departure have direct behavioural consequences (Holland 1986), such as causing changes in the timing of a collective departure.

In large, dispersed groups, acoustic cues may be particularly efficient at transferring social information and reaching a consensus through a quorum mechanism, but the vast majority of experimental evidence here has been limited to *Apis* honeybees. During nest site selection, acoustic cues play a direct role in quorum decision-making, as well as being associated with coordinating and synchronising swarm take-offs. Waggle-dancing scout bees likely convey acoustic information about nest or food location and quality through vibrational wingbeats and sound pulses (Wenner 1962; Michelsen *et al.* 1987; Nieh & Tautz 2000; Łopuch & Tofilski 2020). When a quorum number of scouts have advertised the same nest site, excitatory vibrational ‘piping signals’ are initiated, which are essential in preparing and synchronising swarm take-offs by warming flight muscles (Seeley & Tautz 2001; Seeley & Visscher 2003; Makinson & Beekman 2014). Similarly, inhibitory vibrational ‘stop signals’, which only differ slightly from piping in their acoustic structure (Schlegel et al. 2012), are used to down-regulate waggle dancing and nest site scouting and advertising after a consensus has been reached (Seeley *et al.* 2012). While piping and stop signals do not directly mediate quorum decisions like waggle dances, they are vital in transferring social information rapidly between many individuals to facilitate the decision outcome. Moreover, the relative importance of acoustic cues in mediating waggle dance quorum-sensing has yet to be determined compared to olfactory or tactile cues, which are also methods for dances to encode information (Rohrseitz & Tautz 1999; Thom *et al.* 2007). It is therefore necessary to investigate the role of acoustic cues in quorum decisions in vertebrates, where acoustic communication, such as vocalisations, is often used more conspicuously.

Experimental evidence for acoustically-mediated quorum decisions in vertebrates is limited to meerkats (*Suricata suricatta*) (Bousquet *et al.* 2011). While numerous studies have used playback experiments to highlight the role of vocalisations in collective decision-making by artificially stimulating stronger, more noticeable behavioural responses (Chaverri *et al.* 2012; Suzuki & Kutsukake 2017; Woods *et al.* 2018; Coomes *et al.* 2019; Scarry 2020), to my knowledge only Bousquet *et al.* (2011) explicitly tested quorum decision-making. Here, they played pre-recorded 'moving calls' from one meerkat to a foraging group and compared the change in group movement speed to when control 'close calls' (usually produced to maintain distance between foragers) were played. They found that group movement speed and the likelihood of moving foraging patches increased significantly when 'moving call' playbacks elicited 'moving call' responses from at least one but usually two individuals. However, 'close call' playbacks had no effect on group movement. This indicates that meerkats use specific vocalisations in combination with a quorum mechanism to make consensus decisions, requiring a threshold of at least two but usually three individuals to signal their preference before the group moves off. While this provides important evidence, meerkats are cooperative breeders that live in small, kin groups, so there is less likely to be as many conflicts of interest in decision preferences for group movement compared to non-kin groups, especially as it is vital that meerkat groups remain cohesive for anti-predator benefits (Clutton-Brock *et al.* 1999). Thus, there could be important distinctions to be made between the vocally-mediated quorum mechanisms in small, kin groups and those in large, non-kin groups, where there is more potential for conflicts of interest and causal evidence is lacking.

Jackdaws (*Corvus monedula*) present an ideal study system for investigating the role of vocalisations in the collective decision-making of large groups, with hundreds or thousands of dispersed, mostly unrelated individuals departing winter roost sites simultaneously just before sunrise each day (Coombs 1961). Here, individuals often display a gradual, crescendo-like increase in calling intensity leading up to collective roost departures (Pearce 2012; Bridger 2016; Chapter 2, this thesis). In Chapter 2, I showed that greater rates of increase in calling intensity across an hour period before departure are associated with earlier departures and non-linearly associated with greater departure cohesiveness, with positive rates eliciting sharp increases in the proportion of the roost population that departed together. Similarly, greater absolute calling intensities in the final minute before departure were non-linearly

associated with greater proportions departing together. These results suggest that calling intensity may be interpreted as a proxy for the number of roosting individuals that are motivated to depart at a given time and that collective decisions appear to change significantly when a quorum of calling intensity is reached. Although my observational evidence is consistent with quorum decision-making, manipulative experiments are necessary to determine whether vocalisations play a causal role in coordinating mass roost departures. Bridger (2016) was the first to investigate the potential acoustic mechanisms underpinning collective roost departures experimentally through playbacks. Here, they tested whether low frequency 'primer' calls (<1000Hz) prepare the group for take-off by introducing greater intensities of these calls earlier than they might normally occur. They compared the time of the largest departure when either low frequency calls, high frequency calls (>1000Hz) or control wave noise, played through a loudspeaker immediately prior to the jackdaws' departure. Low frequency playbacks had no effect on departure time compared to other treatments. It is possible that these playbacks were simply unable to introduce a sufficient change in the jackdaws' perceived calling patterns to trigger a noticeable behavioural response, especially considering only one speaker was used and placed at the edge of the roost. Building on Bridger's (2016) study, my findings in Chapter 2 suggest that if departures are triggered by reaching an acoustic threshold, the end of the pre-departure period is likely to be the most sensitive time for playbacks to evoke a noticeable behavioural response.

Here, I used playback experiments to test whether vocalisations are a causal factor in initiating collective roost departures. To do this, I artificially introduced greater intensities of calling towards the end of the pre-departure period using multiple loudspeakers placed within the roost. Based on my findings in Chapter 2, I predicted that departures would occur earlier when experimental calling playbacks were used compared to control wind noise playbacks and no treatment trials of unmanipulated departures. No treatment trials were included to compare playback treatment departures with those occurring under natural conditions, and to reveal whether control playbacks influenced departure time in some way. If greater intensities of calling act as a proxy for a greater number of individuals motivated to leave, the additional calling may act to heighten and synchronise individuals' arousal levels and reach an acoustic threshold faster, leading to earlier departures.

3.2. Methods

3.2.1. Roost Study Site

I conducted all audio recording and playback experiments between Dec 2019 to Mar 2020 from within one jackdaw roost at College Reservoir, Mabe Burnthouse, Cornwall, UK. I chose this roost due to previous observations highlighting it having consistent activity throughout the winter roosting period, making it ideal for maximising the number of possible playback trials as these needed to be spread across many weeks. Moreover, departures here were consistent in their direction and group size (approximately 200 individuals), which enabled me to optimise my data collection positioning and record reliable departure times.

3.2.2. Playback Experiments

Audio recordings and playback construction

To obtain audio recordings of jackdaw calling during the pre-departure period, I programmed recorders to record for 4 hours, starting 3 hours before sunrise. Four SM3 Wildlife Acoustics recorders were used and strapped to trees within the roost at a height of 2.5 m and in a grid 40 m apart. Audio to be used in playbacks was selected exclusively from the recorder with the most sensitive microphones to obtain the highest quality audio available. This was determined by comparing which recorder consistently had the highest average amplitude (dB) across recordings from a sample of five mornings.

To construct experimental playback tracks (N = 10), I used Audacity (www.audacityteam.org) to extract 15-minute samples of jackdaw calling audio. I selected 15 minutes as an appropriate track length to expose jackdaws to sufficient acoustic stimuli for behavioural responses to become noticeable, while also being short enough to ensure that any lasting disturbance was unlikely. To avoid pseudoreplication, playback tracks used different audio for each trial, but within each trial, all speakers played the same track. Playback tracks were sampled from within recordings of the last 30 minutes before the first departure of each morning. This made up a combined total of 25.5 hours of available recordings from 51 mornings under natural roosting conditions. By only using audio from the last 30 minutes before departure, I ensured that playbacks contained calling that gradually increased

in intensity towards a peak at the end of the pre-departure period, as observed with natural mass departures from my audio data in Chapter 2. I applied 6 dB noise reduction to all calling playback tracks in Audacity, which specifically reduced the amplitude of continuous background sounds that were independent from jackdaw calls but existed in the same frequency range. I also applied a high pass filter at 250 Hz to completely remove very low frequency continuous background sounds that were outside of the jackdaw calling frequency range (480-4000 Hz). To create the control wind noise playbacks (N = 10), also 15 minutes in length, sample wind noise was obtained online from www.whitenoisemp3s.com. I selected wind noise as it varies in intensity periodically in peaks and troughs in a similar way to jackdaw calling, and it is a natural sound that jackdaws would be familiar with and not react adversely to. All playback track audio was faded in and out at the beginning and end to avoid a sudden burst of noise and a sharp drop as the audio began and ended, which could disturb the birds.

To further minimise disturbance, playback audio was calibrated to ensure that broadcast calls matched natural jackdaw calling amplitudes. To achieve this, I broadcast samples of calls from each playback track from the speaker and gradually adjusted the volume settings while simultaneously recording the sound with a recorder placed 20m away (mirroring the approximate distance of recorders from jackdaws roosting in trees above). By examining the average root-mean-square (RMS) sound pressure of the resulting recording in Audacity, I could determine the speaker volume setting required to match the natural calling amplitudes recorded in the roost. This calibration method was repeated for matching control wind noise playbacks so that they played at the equivalent RMS sound pressure level as the jackdaw playbacks. Moreover, since my findings in Chapter 2 suggest that an absolute threshold of >-74 dB/Hz (from a distance of 20-40m) is associated with more birds being more likely to depart together, I ensured that playbacks introduced peak amplitudes greater than this threshold.

Playback tracks were carefully constructed to ensure that treatment audio started 20 minutes before the first jackdaws were predicted to depart (playback start ranged from 49-64 minutes before sunrise). This ensured that there would be a 5-minute buffer between the end of the playback and the predicted first departure. Therefore, if birds departed earlier one day because of non-playback influences (e.g. meteorological variables), there would be less of a chance that they would depart

before they were exposed to the full 15-minute track, which could result in birds receiving different treatment lengths on different days. I determined predicted departure times by constructing a linear regression model that accounted for the forecasted conditions of meteorological variables that influence departure time (see Chapter 2), using data collected on departures under natural conditions at the same roost. To ensure playbacks began at precisely the desired time, 15-18 hours of silence were added before the 15-minute treatment audio began. This allowed me to trigger the full playback track (total length: 15-18 hrs of silence, plus 15 mins of treatment audio) in the afternoon, leave the loudspeakers overnight and have them begin automatically in the morning. Therefore, this eliminated the need to get close to the roosting birds to activate the speakers manually, which would risk disturbing them.

Speaker deployment in the roost

Four FoxPro Fury 2 loudspeakers were first covered with waterproofing material (leaving the speaker cones exposed) and attached to external battery packs placed in a waterproof plastic box. Speakers were then strapped to trees within the roost at a height of 2.5 m and in a grid 40 m apart. The grid was positioned so that each speaker would sit roughly halfway between two adjacent recorders. I used a remote control to trigger the playback tracks on all speakers simultaneously while they were placed together on the ground. The time I did this ranged from 15 to 18 hours before the predicted departure, with the appropriate length of silence added to the playback track, depending on when I planned to arrive at the roost. All speakers were collected from the roost the following day and batteries recharged before the next trial. I monitored the position of the roosting birds and kept the speakers in the same position for the first five trials (four no treatment; one experimental). After this, the birds' roosting position shifted 20 m to the south-west, so I moved the speakers to maintain proximity for the remaining 22 trials. To avoid disturbing roosting birds, I set up and took down all recording and playback equipment during the daytime while birds were away.

Experimental design

Playback experiments followed a repeat measures design with the treatment of each trial being selected pseudo-randomly, such that the same treatment was never used more than twice in a row, minimising the risk of habituation to that treatment. To

mitigate continuous disruption to daily roosting behaviour and departure timings, there was at least a one-day gap between trials. I assigned trials to one of three experimental treatments: i) *Control:* Speakers play wind noise audio; ii) *Experimental*: Speakers play jackdaw calling audio; iii) *No treatment*: No playback speakers used.

Mornings where rain was forecasted around sunrise were avoided as observational data shows that rain influences departure times (see Chapter 2). I attempted to conduct ten trials per treatment (total = 30). However, trials were excluded from the analysis when rain occurred before departure, less than three speakers successfully played audio, or departure time could not be determined due to low visibility or arriving too late at the roost. Therefore, overall analyses included 23 trials (eight control, seven experimental and eight no treatment).

3.2.3. Data Collection

To record collective departure times, I observed with binoculars and filmed using a Canon EOS 550D camera with a 70-300 mm lens, starting an hour before sunrise. To avoid disturbance, observations were made from a standardised position 100 m from the roost with a clear view of departures. Collective departures were defined as more than ten jackdaws flying away from the roost at the same time in the same direction, as in Chapter 2. To account for correlation between departure time and sunrise time in corvids (Khadraoui & Toews 2015; Hubálek 2017), I calculated actual departure times relative to sunrise, with negative values indicating minutes before sunrise. Since pilot observations at this roost indicated that often two departures occurred containing roughly even-sized groups (each appearing to consist of >50 individuals), I recorded the times relative to sunrise of both the first and second of these collective departures. Separate departures were distinguished by at least a 15-second gap between when the first departure moved out of view and the second became visible. I was unable to estimate the largest departure (as done in Chapter 2) due to the departures at this roost being particularly early and taking place in very low light conditions, leading to video footage quality being too poor to accurately count the number of birds in each departure. However, since only a maximum of two collective departures occurred, by recording the times of both departures and analysing them separately, I could be certain that one of these was the largest

departure, and therefore my findings here could be appropriately related back to those in Chapter 2.

My findings in Chapter 2 revealed that cloud coverage strongly influences departure time, with barometric air pressure, wind speed, air temperature and air humidity all having suggestive influences, so it was important to account for these as covariates in this study. Data for barometric air pressure (mPa), cloud coverage (%), wind speed (mph), air temperature (°C), and air humidity (%) were obtained for the hour nearest to departure time (either 06:00 or 07:00) for the roost's GPS location through an application programming interface (API) from 'World Weather Online' (www.worldweatheronline.com).

3.2.4. Statistical Analysis

All statistical analyses were conducted in R version 1.1.456 (R Core Team 2018). Multiple linear regression models were constructed and compared, modelling the relative time to sunrise of the first departure as the response variable, playback treatment type as the key explanatory variable and meteorological variables as covariates. Additional multiple linear regression models were constructed and analysed using the relative time of the second departure as the response variable. Simple linear regression models were also constructed for the first and second departure with playback treatment as the only predictor. Residual plots were assessed for violations of model assumptions (Pena & Slate 2006). I tested for multicollinearity between predictors by assessing the variance inflation factor (VIF).

3.2.5. Ethics Statement

This experiment was approved by the research ethics committee at the University of Exeter (reference eCORN000644) and followed the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (2020).

3.3. Results

3.3.1. Playback treatment effects on departure time

The time of the first departure ranged from 50 to 29 minutes before sunrise (mean (± s.e.) = 38.4 (1.1)) and the second departure from 47 to 29 minutes before sunrise (mean (± s.e.) = 36.0 (1.1)).

First departure

The first departure occurred, on average, 5.715 minutes earlier during experimental trials compared to control trials (Table 3.1; Figure 3.1A). In contrast, there was no significant difference between the effects of control and no treatment trials on departure time. Neither cloud coverage nor barometric air pressure had significant relationships with departure time. In a linear regression model where these meteorological variables were excluded, departures occurred, on average, 6.571 minutes earlier during experimental trials compared to control trials (estimate (s.e.) = -6.571 (2.528), 95% CI (lower/upper) = -11.845/-1.298, t = -2.599, p = 0.017). Again, departure time was not significantly different during no treatment trials compared to control trials (estimate (s.e.) = -1.250 (2.442), 95% CI (lower/upper) = -6.345/3.845, t = -0.512, p = 0.614).

Second departure

The second departure occurred, on average, 5.069 minutes earlier during experimental trials compared to control trials (Table 3.2; Figure 3.1B). There was no significant difference between the effects of control and no treatment trials. Neither cloud coverage nor barometric air pressure had significant relationships with departure time. In a linear regression model where these meteorological variables were excluded, departures occurred, on average, 6.089 minutes earlier during experimental trials compared to control trials (estimate (s.e.) = -6.089 (2.380), 95% CI (lower/upper) = -11.053/-1.126, t = -2.559, p = 0.019). Again, departure time was not significantly different during no treatment trials compared to control trials (estimate (s.e.) = -1.625 (2.299), 95% CI (lower/upper) = -6.420/3.170, t = -0.707, p = 0.488).

Table 3.1. Summary statistics for the model predicting the time of the **first** departure from the variables playback treatment ('treat'), barometric air pressure ('baro') and cloud coverage ('cloud') (adjusted R^2 = 0.369).

variable	estimate	95% CI (lower)	95% CI (upper)	s.e.	*t*-value	*p*-value
intercept	53.945	-150.888	258.778	97.497	0.553	0.587
baro	-0.091	-0.289	0.106	0.094	-0.975	0.343
cloud	0.054	-0.031	0.138	0.040	1.339	0.197
treat						
control	0	0	0	0		
experimental	-5.715	-10.893	-0.537	2.465	-2.319	0.032*
none	-2.097	-6.873	2.678	2.273	-0.923	0.368

Table 3.2. Summary statistics for the model predicting the time of the **second** departure from the variables playback treatment ('treat'), barometric air pressure ('baro') and cloud coverage ('cloud') (adjusted $R^2 = 0.262$).

variable	estimate	95% CI (lower)	95% CI (upper)	s.e.	*t*-value	*p*-value
intercept	-3.357	-209.728	203.014	98.229	-0.034	0.973
baro	-0.033	-0.232	0.166	0.095	-0.349	0.731
cloud	0.054	-0.031	0.138	0.040	1.328	0.201
treat						
control	0	0	0	0		
experimental	-5.069	-10.286	0.148	2.483	-2.041	0.056
none	-2.012	-6.823	2.799	2.290	-0.879	0.391

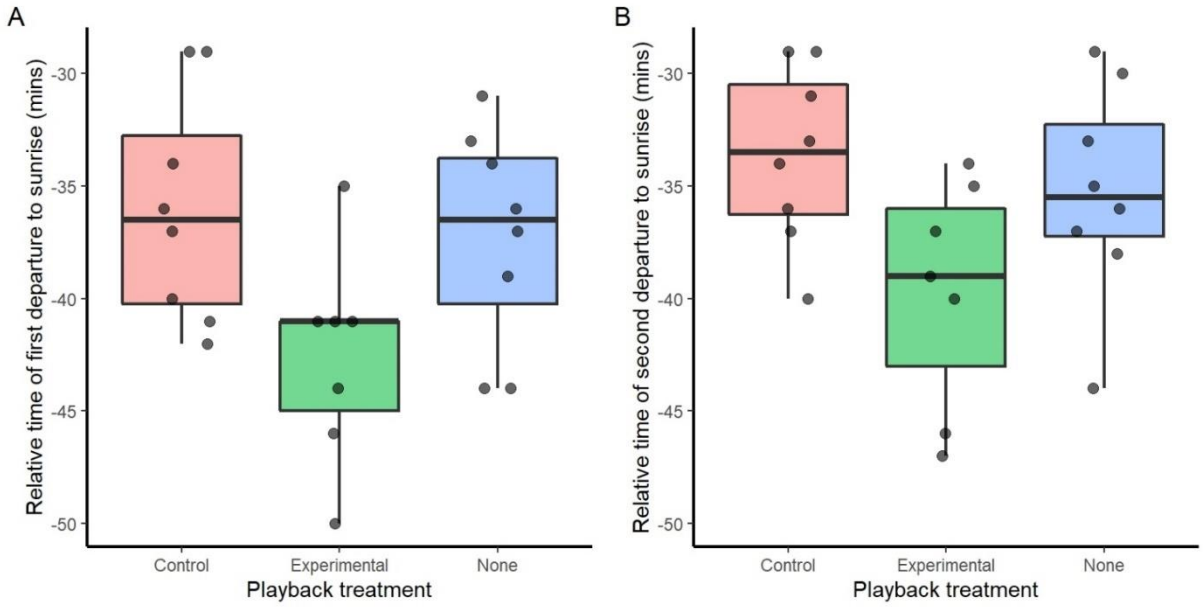


Figure 3.1. Effects of control (wind noise) and experimental (jackdaw calling) playbacks and no treatment trials on the time relative to sunrise of the (A) first and (B) second departure. Box plots display median, quartiles and ranges, along with the raw data.

3.4. Discussion

This study presents the first experimental evidence for vocalisations playing a role in mediating collective decision-making in a large vertebrate group. As predicted, greater intensities of calling introduced by calling playbacks caused departures to occur earlier compared to control (wind noise) playbacks. These results were consistent for both the first and second collective departure in a morning, while also accounting for meteorological variables that influence departure time (see Chapter 2). Moreover, departure timing on mornings with no playbacks did not differ with mornings where control (wind noise) playbacks were played. Together, these results

indicate that earlier departures were caused by birds responding to the conspecific calls in playbacks, rather than simply reacting to increased noise.

These results are consistent with my findings in Chapter 2, supporting my correlational evidence that vocalisations seem to be causally linked to the collective decision-making process. Since either the first or second collective departures was ultimately the largest, and the influence of experimental playbacks was consistent between the two departures, these results can be viewed as largely synonymous with those in Chapter 2, where the largest departure was the primary focus. As my playback experiments demonstrated that jackdaw calling has a causal effect on departure timing, this lends support for my correlational findings in Chapter 2 where earlier departures were associated with faster build-ups in calling intensity. It is possible, therefore, that vocalisations have the capacity to alter the onset of consensus within jackdaw groups. Indeed, in Chapter 2, both the absolute calling intensity immediately prior to departure and the rate of increase in calling intensity were positively and non-linearly associated with more of the roost population departing together, again suggesting that calling is used to reach a group consensus. Whether jackdaws make consensus decisions by responding to an absolute threshold or by detecting the rate of calling build-up remains uncertain, but there may be unmeasured acoustic properties that also play a role here.

While many correlations have been found between increased individual vocalisations and imminent group movements (Stewart & Harcourt 1994; Black 1998; Radford 2004; Ramseyer *et al.* 2009c; Sperber *et al.* 2017; Walker *et al.* 2017), this chapter broadens the limited experimental evidence for acoustic cues causally influencing consensus decisions (Bousquet *et al.* 2011; Makinson & Beekman 2014). Indeed, my findings have highlighted that vocalisation-based quorum mechanisms appear to be shared across very different animal group compositions. Experimental evidence here until now has only been in small, kin meerkat groups (Bousquet *et al.* 2011), contrasting starkly with large, non-kin jackdaw groups that may face greater challenges associated with transferring and integrating social information. Here, to reach a consensus, a greater variety of decision preferences from far more individuals must be integrated. Although corvids have been shown to assess up to 30 different callers in laboratory settings (Ditz & Neider 2016), there may be cognitive limitations on assessing caller numerosity in natural environments where attention must be divided between a greater variety of ecological stimuli (Coomes *et*

al. 2019). This likely to be particularly pertinent in jackdaw roosts where there can be hundreds or thousands of individuals calling at once. My results suggest, however, that vocalisations may act as an effective proxy for identifying a quorum number of supporters in large groups where visual cues and individual caller recognition are restricted as vocalisations can propagate over long distances.

The use of acoustic cues as a proxy for quorum decisions could also have important implications for the 'social feedback' mechanisms involved in the transition from individual to group behaviour in the consensus decision-making of large animal groups (Petit & Bon 2010). Through acoustic cues, social information can be exchanged with great efficiency between many dispersed individuals, facilitating the aggregation of individual preferences to a group-level consensus and promoting synchronised activity (Seeley & Tautz 2001; Visscher & Seeley 2007). Since I was able to experimentally manipulate jackdaw departures to occur 5-6 minutes earlier on average, the consensus decision-making process appears to be flexible directly in response to changes in social cues. It is possible that a vocalisation-based mechanism here allows sufficient flexibility for collective behaviour to be altered according to the day-to-day differences in the aggregation of individual preferences (Stroeymeyt *et al.* 2011). This is particularly important for understanding the ways that animal groups can reach a consensus when the social information individuals possess differs greatly over time (O'Shea-Wheller *et al.* 2017), potentially resulting in conflicts of interest (Couzin *et al.* 2011; Conradt 2012). For instance, some roosting jackdaws may have less up-to-date information on rich feeding locations and so may be more inclined to depart the roost earlier to increase search time without compromising on time spent feeding. Indeed, individuals having met their daily food intake rate sooner appear to arrive earlier at roosts at dusk (Bjeleveld *et al.* 2010), inferring that less successful individuals must spend more time foraging to meet their energy requirements. Conversely, more informed individuals may be less inclined to leave the roost early because they may be more likely to have fed successfully. However, if pooling social information reduces the potential costs of relying on personal information (King & Cowlishaw 2007), uninformed individuals may benefit from following informed conspecifics. For instance, when proportions of informed individuals are higher, uninformed individuals may prefer to leave later to follow informed conspecifics to rich feeding sites instead of splitting off from the group earlier, such as in hooded crows (*Corvus cornix*) (Sonerud *et al.* 2001). Indeed, in raven (*Corvus corax*) roosts, individuals that discovered carcasses were usually the

ones that initiated collective morning departures (Wright *et al.* 2003). In these cases, certain individuals may have disproportionate effects on decision-making depending on the ratio of informed to uninformed group members and the resulting degrees of motivation for departure. Here, vocalisations may be used to accurately convey the degree of individuals' motivation or arousal, such as in ravens (Szipl *et al.* 2017) and across taxa (Linhart *et al.* 2015; Congdon *et al.* 2019), with research even demonstrating corvids can control the onset of their vocalisations (Brecht *et al.* 2019). Consequently, consensus decision-making in large groups needs to be flexible enough to account for day-to-day variation in the degrees to which individuals are informed if preferences are to be averaged effectively and the likelihood of costly group fission minimised. My findings suggest that a vocalisation-based quorum mechanism is an efficient way to promote highly variable individual preferences to a group-level consensus when groups contain large numbers of unrelated individuals.

In future work with the jackdaw roost study system, playback experiments should be repeated across a wider range roosts to determine whether the causal effect I found here is robust across different population sizes, degrees of social cohesiveness and proximity to urban environments. For instance, population size and the strength of social cohesion within a roosting group may influence the extent that vocalisations can efficiently transfer social information between individuals. Therefore, some roosts may not adhere to a vocally-mediated quorum with the same fidelity as the roost in this study. In Chapter 2, I found that roosts varied considerably in population size (ranged from 159 to 1470) and how cohesively birds departed the roost. This may impose different pressures on the consensus decision-making process when information must be spread between greater numbers of dispersed or weakly associated individuals. Similarly, variation in roost proximity to urban environments may subject birds to different influences from artificial light or noise levels. It is worth noting that the one roost this chapter focuses on is located next to a busy road and a supermarket that is brightly lit at night, which may have served to illuminate the jackdaws' flight path. This is what could allow them to depart in very low natural light conditions, as I often observed, potentially meaning that departing even earlier than normal would not incur any additional costs. Therefore, they could be more sensitive to playbacks that simulated an earlier onset of consensus than roosts located in rural areas where departing in very low light conditions could have high energetic costs if visibility was too poor to navigate. If birds are reacting primarily to artificial over

natural light sources, this may also explain the relatively weak effect of cloud coverage on departure time here compared to other roosts studied in Chapter 2.

As anthropogenic light and noise pollution is increasingly being imposed on wild animals (Swaddle *et al.* 2015), it is also not clear to what extent this may disrupt collective decision-making processes. In birds, anthropogenic disturbance is known to have adverse effects, such as greater sage-grouse (*Centrocercus urophasianus*) actively avoiding noisy areas (Blickley *et al.* 2012), or ash-throated flycatchers (*Myiarchus cinerascens*) experiencing reduced breeding success due to increased stress and likelihood of nest abandonment (Mulholland *et al.* 2018). There is evidence that both light and noise pollution can influence avian vocal communication (Dowling *et al.* 2011; Grabarczyk & Gill 2020). For instance, artificial light causes increased vocal activity in nocturnally migrating birds (Watson *et al.* 2016) and increased noise causes earlier dawn vocal choruses in some urban birds (Arroyo-Solís *et al.* 2013). The potential repercussions on the collective decision-making abilities of highly vocal species such as jackdaws are unknown. Future work could compare across urban and rural jackdaw roosts how quickly calling quietens after evening roost arrivals, how quickly calling increases before morning departures, and how prominently birds are calling throughout the night. In urban roosts, flatter calling decreases in the evening and increases in the morning, or more calling throughout the night, could indicate greater levels of disruption to natural vocalisation activity.

In summary, through playback experiments I have found the first experimental evidence for vocally-mediated quorum decision-making in a large vertebrate group, with greater calling intensity just before departure causing earlier collective departures from jackdaw roosts. My results show clear distinctions in departure time between experimental and control playback treatments, with also no clear differences found between control playbacks and natural departures. These findings indicate that jackdaws respond directly to conspecific social cues as a means of coordinating mass departures, with vocalisations potentially acting as a proxy for the number of individuals ready to depart in a quorum mechanism. The role of acoustic cues here could have important implications for the transition of individual to group-level behaviour in large, non-kin groups that must efficiently aggregate highly variable individual decision preferences to remain as a cohesive group. Future work should aim to replicate these findings across a greater number of roosts to determine

the extent that vocalisations can influence departure timing under different group sizes and proximities to artificial light and noise sources.

Chapter 4: *General Discussion*

The field of collective decision-making has been largely dominated by theoretical work, but empirical research is essential for capturing the entirety of individual and environmental heterogeneity that influences group decisions in wild systems (Giardina 2008; King *et al.* 2018). However, studying any form of collective behaviour in the wild is challenging, especially when it involves large groups where it can be difficult to track individual contributions to consensus decisions (Hughey *et al.* 2018). Indeed, experimental manipulation of quorum-based collective decision-making in large groups has been limited to eusocial insects (Franks *et al.* 2003; Seeley *et al.* 2006; Makinson & Beekman 2014), with few exceptions in vertebrates (Bridger 2016). Jackdaw winter roosts provided an excellent study system for investigating the coordination of collective decisions in a large vertebrate group, and whether vocalisations are used to mediate departures through a quorum mechanism.

In Chapter 2, I found observational evidence that vocalisations mediate collective roost departures through a quorum mechanism. Meteorological variables explained around 38% of the variation in departure time data, leaving a substantial amount of variation unexplained. Social factors, such as vocalisations, are likely to account for much of the remaining variance. As predicted, I found that calling intensity generally increased in a crescendo leading up to mass roost departures, which occurred earlier when calling intensity increased at faster rates. This suggests that rapid build-ups of acoustic cues may heighten and synchronise individuals' arousal, thus promoting an earlier consensus for when to depart (c.f. Stewart & Harcourt 1994; Hausberger *et al.* 2020). Similarly, greater proportions of the roost population departed together when calling intensity increased faster. This trend was non-linear and indicative of a quorum relationship (Pratt 2005; Conradt 2012), with a sharp increase in the proportion departing together occurring as the rate of increase in calling intensity became positive. A quorum relationship here suggests that birds become increasingly more likely to participate in a collective movement when more and more group members indicate motivation for departure through starting to call or calling more intensely. It is possible that many individuals distributed over a large area, such as a woodland roost, may be able to gauge the 'collective mood' (Ward & Zahavi 1973) more accurately by responding to relative changes in acoustic stimulation instead of absolute calling amplitudes. However, I also found that the

absolute calling intensity in the final minute prior to departure had a positive non-linear (quorum-like) relationship with the proportion departing together. Here, the probability of birds participating in a collective departure became increasingly greater as calling intensity became >-74 dB/Hz. In contrast with my predictions, calling intensity in the final minute was not a function of group size, suggesting that collective decisions may be coordinated by a fixed, rather than proportional, threshold of calling intensity relative to group size. This corresponds with the fixed quorum number of honeybee waggle-dancers (10-15) required to initiate piping and swarm departures (Seeley *et al.* 2003; 2004). Conversely, these results contradict with other groups that use proportional quorums, such as a threshold of 10% of group members required for a collective movement in whirligig beetles (Romey & Kemak 2018) and sanderling flocks (Roberts 1997). Indeed, when group sizes are highly variable, I would have expected a proportional quorum to ensure that decision speed and accuracy remains optimal across different group sizes. Instead, it is possible that in fission-fusion societies like the corvids that also form mixed species roosts, it may be especially difficult to determine group size and what the relevant proportional quorum should be due to individual sensory limitations. Therefore, further work is essential to understand the contexts in which large animal groups use fixed or proportional thresholds to coordinate collective decision-making.

In Chapter 3, I built on these observational findings by using playback experiments to test whether vocalisations immediately prior to departure causally influence roost departure timing. As predicted, experimental playbacks of jackdaw calling caused departures to occur around 5-6 minutes earlier compared to control playbacks of wind noise, while also accounting for important meteorological influences. Moreover, natural departure times during no treatment trials showed no clear difference with control playbacks. These results indicate that jackdaws were responding specifically to conspecific calls. Indeed, they may have interpreted the greater intensities of vocalisations introduced by playbacks as an indication of a consensus being reached sooner, thus inducing an earlier departure. Previously, logistical and technological limitations have made it hard for researchers to manipulate vertebrate groups (particularly large groups) experimentally to reveal causal effects on behaviour. The only experimental study testing vocalisation-based quorum decision-making has been on meerkats, where groups were small (>20 individuals) (Bousquet *et al.* 2011). In Chapter 3, by using multiple remote-controlled and time-synchronised loudspeakers that allowed precise control over what audio animals were exposed to,

I was able to manipulate the behaviour of a large vertebrate group for the first time. To build on this approach in the future, the introduction of interactive playbacks into behavioural research may allow researchers to ask more detailed questions across a wider range of species, as well as overcoming logistical hurdles like triggering speakers manually. With interactive playbacks, calls are recorded before speakers automatically play back the appropriate stimuli in real time (King 2015), enabling for less manual intervention that can have a much greater potential for disturbance and human error while collecting data. For example, in barn owls (*Tyto alba*), interactive playbacks were used to test individual nestlings' vocal responses when their calls were interrupted by a playback of the mother owl's call, which was only possible through automated and reactive speakers (Ducouret *et al.* 2018). Indeed, interactive playbacks may relieve researchers of the need to manually trigger speakers, which could reduce the potential for human error when attempting to ensure treatments remain consistent across many successive trials. In jackdaw roosts, having speakers that are reactive to fluctuations in calling intensity could allow for more nuanced manipulation of calling patterns within the roost. This could be useful for investigating the role of wave-like calling peaks and troughs in synchronising individuals' arousal levels, or whether calling propagates from different points in the roost in waves of excitation as motivation builds for a collective departure.

Together, my results help to address the call to "re-wild collective behaviour" (King *et al.* 2018) and establish the first empirical and experimental evidence for vocally-mediated quorum decision-making in a large vertebrate group. This thesis presents jackdaw roosts as a much-needed avian addition to previous evidence of the use of acoustic cues in mediating quorum decisions in mammals, such as in meerkats (Bousquet *et al.* 2011) and African wild dogs (Walker *et al.* 2017), as well as in large honeybee colonies (Michelsen *et al.* 1987; Seeley & Visscher 2006). One group characteristic jackdaws share with these examples that may promote the use of acoustic cues is a high likelihood that individuals can experience obscured lines of sight with other group members. This is essential for confirming the motivational states of others and identifying when a consensus has been reached for a collective movement. Indeed, meerkats forage with their head down, so using vocal cues allows them to coordinate movements cohesively and efficiently without incurring the time costs of stopping to look around (Gall & Manser 2017). Moreover, wild dogs may not be able to observe the behaviour of all packmates if they are resting within thick bushes, and thousands of honeybees bunch-up tightly on nests, with many

often performing waggle dances in complete darkness in nest cavities (I'Anson Price & Grüter 2015). Therefore, I suggest that where visual cues may be unreliable, acoustic cues are an efficient means for large or dispersed animal groups to propagate information or communicate individual preferences, and thus reach a consensus and maintain cohesion.

Future directions

While some quorum decisions may be adjusted as group size changes, it is still not clear what drives different species to adopt fixed or proportional quorums relative to group size. In larger groups, the optimal quorum threshold may be relatively higher and require more individuals indicating preference for a particular decision outcome. For example, in three-spined sticklebacks, larger groups required more experimental replica fish to move in a new direction before the whole group adopted that direction when responding to a simulated predator (Ward *et al.* 2008) and moving to a new foraging patch (Ward *et al.* 2012). This may be because individuals in larger groups can benefit more from observing the choices of others and pooling more information to make more accurate decisions (Simons 2004; Ward *et al.* 2008; Wolf *et al.* 2013). Although the higher quorums associated with larger groups may incur greater decision latency (Marshall *et al.* 2006; Chittka *et al.* 2009), these time costs are likely outweighed by a reduction in the likelihood of 'false alarm' errors being amplified (Cresswell *et al.* 2000; Sempo *et al.* 2009). This has been demonstrated in humans through a predator detection experiment (Wolf *et al.* 2013). Here, participants briefly observed an image of a large fish group and had to select an escape response if they saw a fish with seven spines but a stay response if not. To replicate social information pooling, they then answered again after being shown the responses of other participants. In larger groups, the probability of selecting the escape response correctly (true positive) increased and the probability of selecting escape incorrectly (false positive) decreased. This was achieved by adhering to a quorum threshold that sharply increased the likelihood of an individual escaping when the proportion of escape decisions they perceived exceeded the group's average rate of false positive decisions but was lower than the group's rate of true positives. Without a mechanism to reduce 'false alarms', large groups could become highly unstable if they were as sensitive to individual movements as small groups simply because having more individuals increases the likelihood of both true and false positives (Wolf *et al.* 2013).

As large groups can become unstable, species with highly variable group sizes may be expected to utilise proportional quorums to maintain cohesion and optimal decision speed and accuracy regardless of how many individuals are involved (Roberts 1997; Romey & Kemak 2018). Although in Chapter 2 I accounted for highly variable group sizes in jackdaw roosts, I found it had no influence on departure decisions. This suggests that jackdaws may be able to exchange information efficiently enough in large groups that quorums can retain consistently optimal decision speed and accuracy and thus, quorums thresholds exhibit little variability in relation to group size. This parallels findings in studies of transit bird flocks, where individual flight behaviour changes affect and are affected by all individuals regardless of group size or density (Chavagna *et al.* 2010; Ling *et al.* 2019d). Therefore, even in very large groups, social information may propagate just as efficiently as in smaller groups to enable cohesive collective movements. This could explain why jackdaw roost departure decisions may be based on a fixed quorum of calling intensity just before departure, contrary to my initial predictions that a proportional quorum may be more likely. Another explanation might be that if group size or composition change frequently, such as in fission-fusion societies, and individuals are highly spread out, it may be difficult to generate accurate estimates of group size to determine what the appropriate proportional threshold should be. Nevertheless, I was only able to take audio recordings from one very large roost (>1000 birds), so further work on more roost sites is needed to confirm with more certainty whether quorum decisions in jackdaws are related to group size. Further playback experiments that vary the amplitude of calling playbacks may also be able to reveal the adherence to an absolute acoustic quorum threshold immediately prior to departure. Research across a range of species, social contexts and group sizes is needed to better understand the conditions under which fixed or proportional quorums are favoured.

As group size changes, so can group composition, which has been shown to affect collective movement decisions in a variety of contexts, but its influence on collective roost departures is yet to be determined. Indeed, variation in social relationships, species identity and dominance can all influence collective movements. For instance, the extent of social affiliation between decision-initiating individuals and other group members may strongly influence the magnitude of the emergent group response (Woods *et al.* 2018). In jackdaws, the attention individuals pay to others and how they coordinate collective movements likely depends on personal association

strength, social rank, sex and colony membership (Woods *et al.* 2018). Indeed, jackdaw pairs are known to stay close together while in large flocks, but more pairs can reduce the efficiency of social information transfer as paired birds pay more attention to their partner than other group members (Ling *et al.* 2019c). Therefore, roosts where group members are less personally associated with each other or the number of pairs is higher might experience less efficient information transfer. This could make it more difficult to reach a consensus on departure timing, resulting in a greater likelihood of group fission. In mixed species corvid flocks, species identity can greatly influence collective movement decisions, with birds preferentially associating with conspecifics and larger, more dominant rooks usually occupying the front edge of the flock (Jolles *et al.* 2013). It is possible that jackdaws departing roosts that contain more rooks might be similarly subordinated by rooks exerting stronger influences on departure timing. Intraspecifically, dominant individuals may also have disproportionate influences on intraspecific collective decisions. In African wild dogs, for instance, when the most dominant individuals initiated a group departure, they reduced the quorum threshold number of individuals required for the whole group to participate (Walker *et al.* 2017). It is possible that in the complex social dominance networks of jackdaws (Kings 2018), more dominant individuals may be able to manipulate collective departure timing in their favour when they are highly motivated to leave at a particular time. Disproportionate influences were found in dominant male baboons (*Papio ursinus*) that consistently led movements towards highly localised and contest-competitive food sources, at which dominants would benefit more since food access order positively correlates with social rank (King *et al.* 2008). However, in large groups like jackdaw roosts, there may be greater individual variation in social information and decision preferences, making it difficult for dominant individuals to recruit followers to their specific preferences.

Similarly, individual variation in personality, body size, age and knowledge are also known to influence collective movement decisions, but again, it is unclear what effects they might have in the context of avian roost departures. Firstly, bolder, more impulsive individuals can disproportionately influence collective decisions (Burns & Rodd 2008; Chittka *et al.* 2009). For example, bolder sticklebacks are more likely to initiate collective movements (Harcourt *et al.* 2009). Although shyer fish prefer to follow leaders of a similar personality, bolder fish can usually overrule this and impose leadership by means of increased activity patterns and a greater propensity to attract others' attention (Nakayama *et al.* 2016). These individuals may therefore

prefer faster decision-making with lower quorum thresholds. However, it is unclear whether greater numbers of bolder individuals could influence decisions in large groups, such as by exerting greater pressure for faster decisions and earlier departures in jackdaw roosts. Moreover, individuals with larger body sizes can be more likely to attract the attention of followers to collective movements, such as in guppies (*Poecilia reticulata*) (Bierbach *et al.* 2020). In jackdaws, the reverse might be true. Smaller individuals with relatively small gizzard sizes, which digest food more slowly, may prefer earlier roost departures as they would need to spend more time at foraging sites to meet their daily intake requirement (Bijleveld *et al.* 2010). Individuals may also prefer to follow those with similarly sized gizzards as birds with smaller gizzards foraging among larger-gizzard birds would face a difficult trade-off: continue to forage as others left but increase vulnerability to predation, or leave unsatiated (Bijleveld *et al.* 2010). Lastly, older, more experienced individuals, such as African elephant matriarchs (McComb *et al.* 2001, 2011), often lead collective movement decisions. Similarly, in corvid roosts, the timing of departure may vary depending on the ratio of informed and uninformed individuals. For example, in hooded crows (*Corvus cornix*), greater proportions of informed individuals are more likely to inadvertently attract more uninformed individuals when departing communal roosts (Sonerud *et al.* 2001). It is also possible that older birds may possess more knowledge of the seasonal fluctuations in local foraging opportunities and their locations.

Although there are many potential effects of group composition on collective decision-making, further work is needed to determine the extent that it can influence avian roost departures. For instance, smaller jackdaw roosts (>200 birds) could be used to investigate which individuals initiate departures as individual preferences here may hold comparatively much greater weight on the decision outcome. This could then be related back to parameters such as species, social rank, individual personality variation, body weight, age and sex. Potentially, this could involve attaching bio-loggers to a number of individuals and tracking the time each begins to fly off in morning roost departures (Fehlmann & King 2016; King *et al.* 2018). Back-mounted microphones have previously been used in jackdaws and may offer a means to track not only movement patterns, but also individuals' calling behaviour and the context that it occurs in (Stowell *et al.* 2017; Gill *et al.* 2020). This could reveal the extent that variation in individual traits, calling intensity and the likelihood of initiating collective departures are inter-related. Tracking individual movement and

calling patterns could also provide insight into whether jackdaws that possess more information about foraging opportunities can have disproportionate influences on roost departures. For instance, birds arriving earlier at the roost may have successfully met their daily food intake and have knowledge of rich feeding sites (Bijleveld *et al.* 2010). Therefore, uninformed individuals may wait to follow informed conspecifics, as found in other corvid species, such as ravens (Wright *et al.* 2003) and hooded crows (Sonerud *et al.* 2001). If individuals that arrived earlier also initiate collective departures or call more intensely, then this could be evidence for information differences having a direct influence on consensus decision-making. This could be tested experimentally by provisioning certain individuals at feeding stations using 'radio frequency identification' (RFID) tags (Bonter & Bridge 2011; Kings 2018). Here, investigations could be made into whether provisioning and access to social information cause changes in individuals' contributions to calling and the following response of others in relation to the fed (informed) individuals.

While my thesis provides strong evidence that vocalisations are used to coordinate collective roost departures in jackdaws, it is still unclear how vocal cues propagate social information through many individuals to enable them to perceive a consensus. It has been well established that through repeated local interactions and exchanges of social cues, group members can exceed their own sensory capabilities and together resemble a 'collective mind' (Couzin 2007; 2009). As such, individuals can achieve effective long-range communication with other group members, which facilitates the rapid spread of activity waves throughout the group (Boi *et al.* 1999; Procaccini *et al.* 2011; Sonoda *et al.* 2019). This is crucial for achieving cohesive and coordinated collective movements across taxa (Couzin & Krause 2003), from the rapid reinforcement of and recruitment to shorter foraging paths by trail pheromones in ants (Deneubourg *et al.* 1990) to the collective turns of large bird flocks (Ling *et al.* 2019a; Storms *et al.* 2019). The amplification of activity waves, particularly in eusocial insects, has been likened to the functional organisation of neural systems in vertebrate brains (Passino *et al.* 2008). Indeed, active ants can 'excite' inactive ants and cause them to also start moving after a threshold of repeated interactions, resembling the firing of a neuron after depolarisation in brain synapses (Cole 1991; Boi *et al.* 1999; Couzin 2009). Moreover, this activity spread can be dampened if excitation is not reinforced, with ants then entering a short refractory period with low excitation probability (Couzin 2009). Similarly, honeybees choosing a new nest site use acoustic piping signals to amplify (Seeley & Tautz 2001; Visscher & Seeley

2007) or stop signals to inhibit (Seeley *et al.* 2012) collective activities. In jackdaws, I have observed that calling often builds in intensity leading up to departure (see Chapter 2), suggesting that as more individuals become motivated for a departure, the transfer of social information becomes amplified through greater vocal cue production. It is therefore possible that vocal cues may possess allelomimetic or 'infectious' qualities, whereby more birds calling increases the likelihood of nearby individuals also starting to call (Gautrais *et al.* 2007). This could spread waves of excitation throughout the group that synchronise the activity of individuals and the final collective departure. Indeed, my audio recordings show that calling follows wave-like patterns where the intensity builds and dampens repeatedly over time (see black lines in Figure 2.1). Departure may potentially then be triggered when calling intensity surpasses an absolute acoustic threshold, as suggested by my findings in Chapter 2. What is yet to be determined is whether waves of calling intensity change as departure approaches, potentially becoming more frequent and reaching higher wave amplitudes as more group members become aroused and motivated for departure. Future research should also investigate the directional properties of how calling spreads through the group and how correlated calling is at different positions in the roost at a given time. If calling is used to reach a consensus, I would expect that calling would spread directionally outward from 'vocal hotspots' (Gall & Manser 2017) that emerge from particularly motivated individuals and become more correlated across different areas of the roost leading up to a departure.

As well as the rate of call production in a group, the acoustic structure of calls may be important in collective decision-making. For instance, African elephants (*Loxodonta africana*) produce a variety of calls and rumbles depending on social context that involve changes in call frequency (Hz) and sound pressure level (dB) (Poole 1988). Similarly, meerkat calls vary according to predator type and the urgency of the intended response, whereby higher urgency calls were of higher frequency (Hz), were louder and lasted longer (Manser *et al.* 2001). In Canada geese (*Branta canadensis*), low frequency calls build and appear to act as 'primers' for collective departures before a switch to high frequency 'releaser' contact calling occurs as a departure is triggered (Raveling 1969). In jackdaws, the build-up of low frequency (>1000 Hz) primer calls was investigated with experimental playbacks by Bridger (2016) for their effect on roost departure timing. However, they found no support for their prediction of low frequency call playbacks causing earlier departures, with no clear differences to high frequency call playbacks or natural

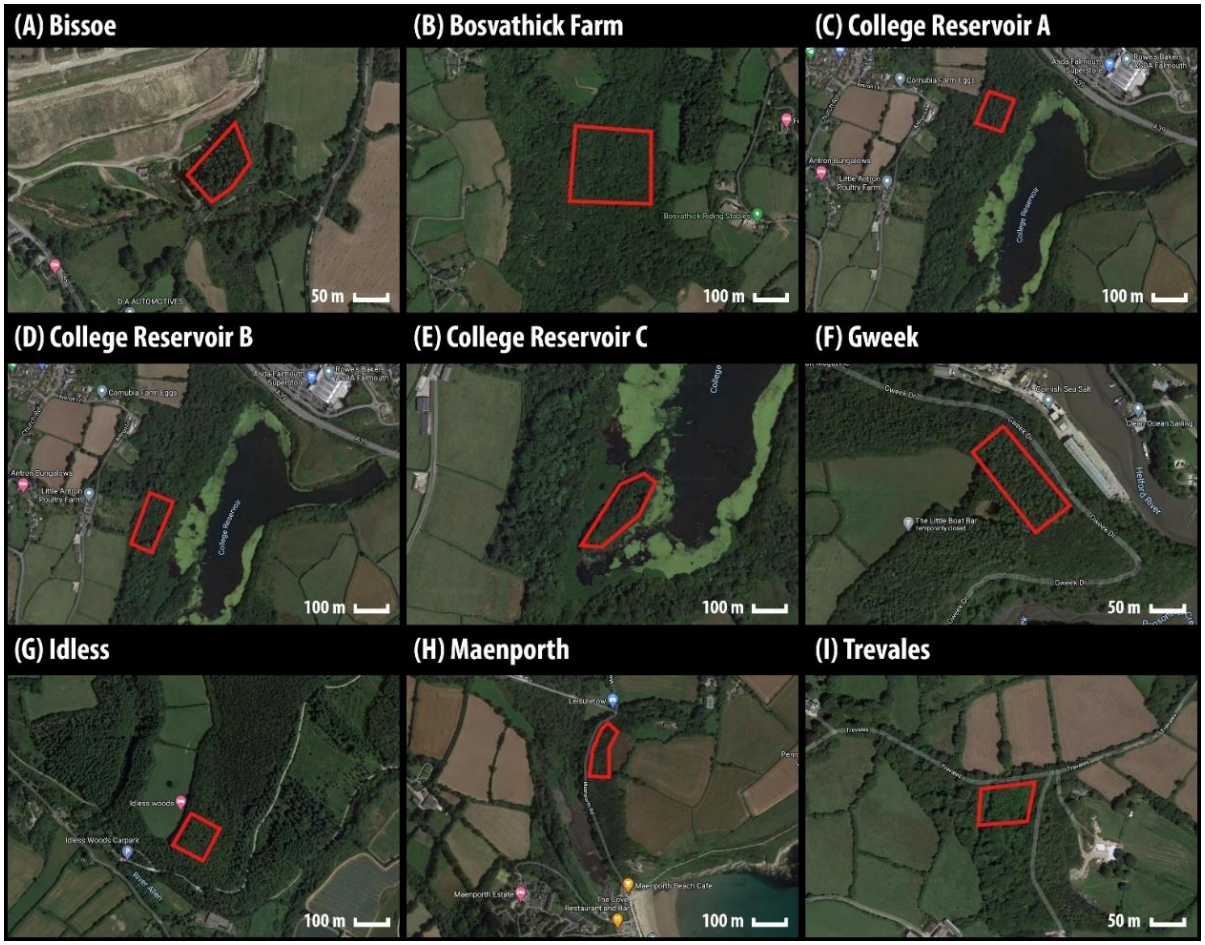
conditions. Nevertheless, future work should build on Bridger's (2016) study to determine whether the acoustic structure of jackdaw calls changes closer to roost departures. If there is a switch in call frequency at departure, this may be what is triggered by birds perceiving an acoustic quorum of primer calls. Indeed, when a consensus is perceived, birds may rapidly switch to releaser call production, just as ants rapidly switch from tandem runs to physically carrying nestmates when a quorum number of ants have aggregated at a new nest site (Pratt 2005). Moreover, back-mounted microphones (Stowell *et al.* 2017; Gill *et al.* 2019) could reveal to what extent individual jackdaws also increase the amplitude of their calls closer to departure, or if they simply call more frequently.

Summary

Research into the role of acoustic cues coordinating collective decisions through quorum mechanisms has been limited in wild systems. In jackdaw winter roosts, I found that mass roost departures occurred earlier and contained greater proportions of the roost population when calling intensity increased leading up to departure. The likelihood of individuals participating in a collective departure increased sharply and non-linearly when rates of increase in calling intensity became positive, but also when calling intensity surpassed an absolute threshold in the final minute prior to departure, indicative of a quorum relationship. Through playback experiments, I also found that vocalisations appear to have a causal effect on roost departures, with playbacks introducing greater calling intensities just before departure causing earlier departures on average. This suggests that greater calling intensity may reflect individuals reaching a consensus and committing to a collective movement sooner than normal. Overall, my thesis presents the first empirical and experimental evidence of vocally-mediated quorum decision-making in a large vertebrate group. Future work should focus primarily on replicating the findings of this thesis across a greater number of roost sites of varying total population sizes, as well as investigating the influence of individuals characteristics and social relationships on quorum decision-making that may vary across different roosts.

Appendix

Maps of roost sites



Google Maps satellite images of roost sites in Cornwall, UK: (A) Bissoe, Truro (50.234010, -5.120804); (B) Bosvathick Farm, Constantine (50.129463, -5.153635); (C) College Reservoir, Penryn roost A (*focal roost in Chapter 3*) (50.161605, -5.127369); (D) College Reservoir, Penryn roost B (50.159185, -5.128978); (E) College Reservoir, Penryn roost C (50.157061, -5.128171); (F) Gweek, Helston (50.091692, -5.206343); (G) Idless Woods, Truro (50.290843, -5.059061); (H) Maenporth, Falmouth (50.129873, -5.095376); (I) Trevales, Truro (50.178374, -5.157890). Areas highlighted by solid red lines indicate estimated roosting jackdaw locations.

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